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A review of research on the impacts of sediment, nitrogen, and phosphorus on aquatic biota was performed to determine the influences of sediment and nutrients on biota, to suggest directions for future research, and to provide suggestions for management of freshwater systems across the United States. This report is divided into two sections. The first section provides an organization and background information to enable incorporation of large amounts of available information and allow assessment of impacts at several hierarchical levels. Included are a hierarchical scheme that is the foundation of the analytical study; a regional analysis of the concentrations of sediment, nitrogen, and phosphorus in surface waters; a review of biotic impact assessment approaches; and a review of modeling of sediment and nutrient impacts. The second section reviews the impacts of sediment, nitrogen, and phosphorus on biota, integrates this information into the hierarchical scheme developed in the first section, and shows how the hierarchical scheme can be used for impact analysis.

The need for a holistic approach to the problems of sediment and nutrient impacts on surface water led to the development of an organizational scheme. This scheme incorporates a nested hierarchy of ecosystems combining geographical and biological units plus their environments at different levels of complexity. The levels used are nation, region, watershed, community, population, and individual ecosystems.

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October 1979

IMPACTS OF SEDIMENT AND NUTRIENTS ON BIOTA IN SURFACE WATERS OF THE UNITED STATES

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FOREWORD

Environmental protection efforts are increasingly directed towards preventing adverse health and ecological effects associated with specific compounds of natural or human origin. As part of this Laboratory's research on the occurrence, movement, transformation, impact, and control of environmental contaminants, the Environmental Systems Branch studies complexes of environmental processes that control the transport, transformation, degradation, and impact of pollutants or other materials in soil and water and assesses environmental factors that affect water quality.

Nonpoint sources of water pollution have received increased attention in recent years as efforts to reach national water quality goals have grown stronger. Sediment and nutrients from these sources are of particular concern because of their adverse effects on plant and animal life in surface waters. This report reviews the current research on the impacts of these pollutants and presents an ecological and geographical scheme for evaluating their effects in freshwaters throughout the United States.

David W. Duttweiler
Director
Environmental Research Laboratory
Athens, Georgia

ABSTRACT

A review of research on the impacts of sediment, nitrogen, and phosphorus on aquatic biota was performed to determine the influences of sediment and nutrients on biota, to suggest directions for future research, and to provide suggestions for management of freshwater systems across the United States. This report is divided into two sections. The first section provides an organization and background information to enable incorporation of large amounts of available information and allow assessment of impacts at several hierarchical levels. Included are a hierarchical scheme which is the foundation of the analytical study; a regional analysis of the concentrations of sediment, nitrogen and phosphorus in surface waters; a review of biotic impact assessment approaches; and a review of modelling of sediment and nutrient impacts. The second section reviews the impacts of sediment, nitrogen, and phosphorus on biota, integrates this information into the hierarchical scheme developed in the first section, and shows how the hierarchical scheme can be used for impact analysis.

The need for a holistic approach to the problems of sediment and nutrient impacts on surface water led to the development of an organizational scheme. This scheme incorporates a nested hierarchy of ecosystems combining geographical and biological units plus their environments at different levels of complexity. The levels used are the nation, region, watershed, community, population and individual ecosystems.

Management of water quality throughout the United States based upon the same set of criteria or standards does not adequately predict biotic responses to nutrient and/or sediment additions in many situations, and regulations can be too restrictive in other situations. Since it is not feasible to manage each water body independently, a regional approach to management is examined. The conterminous United States is divided into the 23 "Province" levels of the Bailey Ecoregion Classification System, a scheme based on differences in climate, soil type and vegetation. Concentrations of phosphorus and nitrogen obtained during the National Eutrophication Stream Survey and sediment concentrations from past stream surveys are examined for regional trends. Regional patterns of land use and water hardness are identified. Sediment and phosphorus concentrations are correlated positively with each other and with land use patterns. Areas of intense agriculture have the highest levels of sediment, nitrogen and phosphorus. Similar information on lakes throughout the United States is needed in order to determine the geographical patterns that might be useful in management.

Methods for assessing water quality through biotic variables are reviewed. An evaluation is made of the usefulness of impact indices and other methods of describing the structural and functional interrelationships of communities and the most appropriate indices for each hierarchical level are identified. Also, coarse and fine resolution models of freshwater ecosystems are reviewed to show the strengths, weaknesses, current status, and trends in modelling efforts and to stress the usefulness of the models in predicting impacts.

The impact of sediment in freshwater systems is examined. Additions of sediment are shown to affect the biota at all trophic levels. The degree and type of impact depends not only upon the concentration but also upon sediment particle size. Although a continuum of particle size of sediment exists, biotic impacts are different at the two extremes--bed load and suspended sediment. Bed load movement damages benthic organisms through scour, abrasion, and burial; suspended sediment increases turbidity and, therefore, may decrease photosynthesis and impair visibility for sight predators. Sediment loading may best be managed by prevention of soil erosion on watersheds. Other management strategies include the use of mitigating structures to slow bed load movement and provide habitats and the use of chemicals to precipitate suspended sediment.

Phosphorus and nitrogen forms, cycling and typical concentrations are discussed in relation to their roles in aquatic systems. Research on experimental addition of nutrients to water bodies is reviewed and organized by trophic state of the water bodies, since the impact of added nutrients depends upon initial conditions. The usual biotic response to nutrient addition is a stimulation of primary production leading to eventual eutrophication. A standard sequence of events with increasing eutrophication is presented and management strategies discussed. Water bodies may be managed at a coarse level of resolution by regulating nutrient loading in relation to water retention time. However, phosphorus loading models, which have been used for many lakes, do not always predict biotic response well, implying the need for nitrogen loading models in nitrogen limited systems. The coarse resolution methods also make predictions based primarily on hydrology, neglecting the biology of freshwater systems. Biological considerations may be important in some systems and, in others, management of particular species of interest may be needed.

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CHAPTER 1

INTRODUCTION

Sediment and nutrient inputs into waters of the United States have received considerable attention in the past few decades. Inputs as point sources of pollution received initial attention, and more recently non-point sources have received the emphasis. Extensive efforts have been conducted by state and federal agencies to identify sources of sediment and nutrients, to determine ameliorating management practices, and to establish regulations to reduce inputs. However, the extant information on impacts of sediment and nutrients on biota in surface waters of the United States has not been synthesized or organized in a meaningful manner. Also, there has been little effort to direct research in a manner that will provide quantification of impacts for the entire country.

This report examines the impacts of sediment and selected nutrients on biota in the freshwaters of the continental United States, excluding Alaska. Sediment is reviewed because of its roles in increasing turbidity--particularly in streams having disturbed watersheds, in physically damaging organisms, and in acting as a carrier of nutrients. Phosphorus and nitrogen are selected because they are implicated as the major nutrients associated with lake eutrophication, because inputs are derived from nonpoint as well as point sources, and because inputs to water bodies are increasing through activities of man. The few broad geographical analyses of data on lakes and reservoirs from the tropics to the arctic have indicated that nutrient availability is a predominant factor regulating primary productivity (Brylinsky and Mann 1973; Schindler 1978).

Analysis of sediment and nutrient impacts requires development of a framework of organizing principles. The first section of this report includes several chapters which develop this framework. Chapter 4 is concerned with semantic and conceptual issues. Some ecological terms are defined and a hierarchical scheme is presented which provides organization and allows integration of large amounts of information. One level of the hierarchy, the region ecosystem, is examined in Chapter 5 as a possible level for management of water quality. Regions of the United States are examined as areas of similar climate, soil type, water chemistry, and land use which, therefore, may exhibit similar responses to nutrient or sediment additions. In Chapter 6 methods of assessing water quality through biotic variables are reviewed. An evaluation is made of the usefulness of impact indices and other methods of describing the structural and functional interrelationships of communities. The last major chapter of this section, Chapter 7, reviews approaches to modelling freshwater system behavior at coarse and fine levels. Chapter 8 provides a short summary of the organizing concepts underlying the report.

The second section of the report includes two chapters, 9 and 10, which review the information on the roles of sediment and nutrients in freshwater and their impacts on biota. Chapter 11, the final chapter, integrates the two parts of the report. The biotic impacts of sediment and nutrients are evaluated by the ecological hierarchy that was established and the applications of coarse and fine modelling approaches are discussed. Within these chapters descriptive models at various levels are included which integrate biotic and abiotic components and which can be examined from a structural or a more dynamic functional aspect.

The scientific objective of the report is to determine if, at specified levels of organization, the response of biota to given inputs of sediment and nutrients in freshwater systems can be predicted. The adequacy of the information base is evaluated, the confidence or certainty of understanding of aquatic dynamics is determined, and directions for future research are suggested. Hopefully, the results presented here will assist in developing more efficient research programs and will lead to more effective management of the aquatic environment.

1.1 LITERATURE CITED

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Schindler, D. W. 1978. Factors regulating phytoplankton production and standing crop in the world's freshwaters. Limnol. Oceanogr. 23:478-486.

CHAPTER 2

CONCLUSIONS

2.1 GENERAL

A. The impact of sediment and nutrients on freshwater biota can be evaluated at any of several levels of a hierarchy of ecological organization. For this report we have adopted a hierarchy of freshwater ecosystems including the nation, region, watershed, community, population, and individual.

B. Feasible management of freshwater biota requires evaluation at higher levels such as the nation or region.

C. The adoption of nationwide water quality standards may be inexact for certain waters and rigid for others. Regional standards may ameliorate this problem.

D. Methodology must be standardized to allow comparisons between regions.

E. Weaknesses exist in the available data on the effects of nutrients and sediment on aquatic biota. Whole system studies are few, research has not been well distributed within the United States, and information is lacking on the variability of the response for different system types and different trophic states.

2.2 REGIONALIZATION

A. The Bailey Ecoregion Classification System was examined as a means of regionalization. The "province" level of this classification was used since it integrates climate, soil, and vegetation. Regional patterns of nutrients and sediments are most strongly correlated with land use practices and, thus, do not correspond well with "province."

B. Using available information on nationwide stream characteristics, (Omernik; Rainwater; and Geraghty et al.) regional patterns of baseline sediment, phosphorus, and nitrogen concentrations; land use; and water hardness were identified.

1. Nitrogen concentrations in rivers of the United States are predominantly low, phosphorus concentrations are predominately high, and sediment concentrations are variable depending upon the region of the country.

2. High and medium sediment concentrations are correlated with high or medium phosphorus concentrations in approximately half of the United States.

3. High sediment correlates positively with nitrogen only in areas of high agricultural use.

4. Concentrations of phosphorus and sediment are associated with land use practices. Intensive agricultural areas have high sediment and phosphorus concentrations in rivers; intensively forested areas generally have low sediment and nitrogen concentrations in streams.

5. Patterns of water hardness were identified as a possible influencing factor on biotic response.

C. Baseline information is available for some streams, lakes and impoundments. However, regional comparisons have not yet been done.

2.3 IMPACT ASSESSMENT

A. The set of biotic and abiotic variables used to assess nutrient and sediment impacts depends on the level of ecological organization chosen for study. At high levels of organization, variables indicating the level of primary and/or secondary productivity are of greatest interest. At lower levels species behavior, tolerance, and abundance may be most useful.

B. Emphasis on functional variables as measures of aquatic response identifies dynamic ecosystem properties, allowing a higher scale evaluation of the effects of perturbation.

2.4 MODELLING

A. Models have been developed to predict response at different levels of resolution. Coarse resolution models may predict gross effects of nutrient or sediment loading but do not work well in spatially diverse systems. Fine resolution models require a great deal of specific information but describe dynamic system properties.

1. The MS. CLEANER model of the Eastern Deciduous Forest Biome represents the state-of-the-art in fine resolution lake modelling. It is complex and expensive to run in its entirety; however, it is constructed in modular form and only parts of the model may be required to answer specific questions. McIntire and Colby's hierarchical stream model represents the state-of-the-art in fine resolution models. It does not yet include nutrients and can only be used for stream orders 1 - 4.

2. Many coarse resolution models have been developed for lakes and streams. Adaptations of Vollenweider's lake models and Streeter and Phelp's stream model have been most widely used.

B. Models are applicable to impact assessment:

1. Perturbation analysis can be used to describe behavior of systems to which pollutants have been introduced.

2. Sensitivity analyses can identify parts of an ecosystem most sensitive to impact.

3. Stability analyses can evaluate how quickly a system will respond to impact and then return to normal behavior.

4. Flow analysis may suggest how nutrient and sediment inputs can be adjusted to give desired system behavior.

C. Limits of use of models:

1. To date models have been developed only for well mixed systems and do not describe marshes, swamps, and littoral regions well.

2. The inability to adequately characterize inputs, particularly from nonpoint souces, limits predictability of models.

3. Temporal variations in system behavior often are not considered in coarse modelling approaches.

4. The statistical significance of relationships observed through modelling cannot be established.

2.5 SEDIMENT

A. A continuum of sediment size exists, although the two size extremes have different impacts on biota.

1. Suspended sediment generally exerts an indirect impact on biota and is most important in slower moving waters (lakes, reservoirs, some streams).

2. Bed load sediment exerts a direct impact on all benthic organisms and is significant only in rapidly flowing water.

B. Sediment has an impact on all trophic levels.

1. Suspended sediment increases turbidity, thereby reducing light availability to primary producers and limiting

visibility for sight predators. Clogging of filtering structures in molluscs also can occur.

2. Bed load movement scours, abrades, and buries benthic organisms; it also modifies habit structure.

3. Effects of sediment may be propagated through the food web or may result in movement of organisms out of the area.

C. Sediment may carry nutrients, particularly phosphorus, offsetting some of the detrimental effects of sediment to the extent that productivity may be stimulated.

D. The major impact of sediment is associated with storm events or snow melt which occur infrequently

E. Management of sediment may be accomplished by:

1. Control of surface erosion

2. Use of mitigating structures in altered channels to provide habitat for organisms.

3. Precipitation of suspended sediment by the use of chemicals.

2.6 NUTRIENTS

A. The principal impact on biota is the stimulation of primary production in nutrient limited systems. Stimulation results from the addition of the nutrient needed for growth that is in shortest supply relative to growth needs of most organisms.

B. In detrital based systems nitrogen addition increases secondary production by stimulating decomposition.

C. Indirect impacts of nutrients on higher trophic levels primarily occur in three ways.

1. Higher trophic levels can be stimulated by an increase in primary production propagated through the food web.

2. Species composition and production may be modified by changes in the food web.

3. Variation in primary production may cause changes in the physico-chemical environment which influence the production and composition of higher trophic levels.

D. The standard aquatic response to increased nutrient input is an increase in the rates of nutrient transformations. Internal nutrient sources from increased biotic cycling and from exchanges with sediments may increase significantly epilimnetic nutrient levels, especially in more eutrophic systems.

E. Regulation of nationwide productivity might be accomplished by employing Dillon's or Larsen's and Mercier's critical nutrient loading levels based on hydraulic residence time (dilution). These levels were developed for phosphorus limited systems; applicability to systems limited by other nutrients has not been investigated.

F. Management of a particular biological species may be accomplished by:

1. Regulation of consumer trophic levels which have a large degree of control over lower levels.
2. Control of blue-green algae by decreasing pH, adding nitrogen or carbon dioxide, or perhaps by mixing.
3. Manipulation of nutrient ratios which may result in a shift in dominant species (works in theory but is unpredictable in practice due to numerous interrelated factors).
4. Maintenance of a high level of water quality for a species of interest in specific water bodies.

CHAPTER 3

RECOMMENDATIONS FOR RESEARCH

3.1 GENERAL

A. Make use of existing information on nutrient and sediment concentrations to evaluate the general condition of the nation's waters and to establish the relationship between concentrations observed in standing and flowing waters.

B. Obtain more nationwide data, including information on a variety of system types and trophic states.

C. Group waters by similarities for management through use of existing data storage systems such as STORET or NAWDEX.

D. Make information contained in government publications and in STORET more accessible to academicians.

E. Determine if individual monitoring of waterbodies for particular species of interest is necessary.

3.2 HIERARCHICAL ANALYSIS OF FRESHWATER SYSTEMS

A. Conduct future research in a more holistic manner, considering interactions within and between communities.

B. Utilize performance curves to a greater degree as visual descriptors of migrating phenomena.

C. Apply a hierarchical scheme of organization to analyses of compiled data on a variety of geographical and biological factors influencing aquatic system behavior and make use of the hierarchy to guide proposed research.

3.3 REGIONALIZATION

A. Investigate possible regional management schemes to allow accurate prediction of system behavior without necessitating management for individual systems.

B. Conduct whole system studies of sediment and nutrient impacts in dissimilar areas of the United States. Such a comparison will help determine the limits within which entire systems respond.

C. Conduct explicit studies of the impacts of sediment and nutrients on biota in the Southeast, Midwest, Southwest, and Pacific Northwest. Only a few impact studies have been conducted in these areas; such studies are needed to test the validity of our regional scheme for categorizing impacts on biota.

3.4 IMPACT ASSESSMENT

A. Standardize environmental indices for evaluating and predicting impacts for different system types and hierarchical levels. These indices should incorporate variables influencing community structure and function. Higher level indices should reflect watershed activities, biotic influences, and water quality.

B. Evaluate the classification of stream ecosystems by the river continuum and dominant functional group concepts to determine if impacts on biota of running waters can be better predicted and managed.

3.5 MODELLING

A. Develop models for poorly mixed aquatic ecosystems such as littoral zones, marshes, swamps, and ponds.

B. Couple watershed models to community models to simulate time varying inputs of nutrients and sediment and to characterize nonpoint source inputs.

C. Evaluate the applicability of macroscopic modelling approaches, such as those by Odum, Patten, and Vollenweider, Larsen and Mercier, and Dillon, to complex aquatic ecosystems. These approaches may be able to answer questions about impact in complex systems more quickly, efficiently, and economically than some of the fine resolution models being developed.

3.6 SEDIMENT

A. Obtain predictive information on the response of primary producers to sediment through productivity measurements that account for temporal variation in flow and the degree to which sediment is suspended or moved.

B. Obtain more information on the effects of surface sealing by sediment on the hyporheal (below the surface) habitat.

C. Study the effect of sediment on the reproductive success of macroinvertebrates.

D. Obtain more information on the degree to which sediment impacts at any trophic level influence other organisms.

E. Improve methods to estimate benthic productivity in systems having an unstable substrate. Presently it is difficult to estimate mortality or damage to any trophic level due to bed load movement.

F. Since storm events and rainfall patterns significantly influence sediment inputs, systems within one region may respond similarly to sediment loading. Regional studies are needed to confirm or reject this idea.

3.7 NUTRIENTS

A. Test the predictability of phosphorus loading models which incorporate phosphorus retention capacity to predict eutrophication on a variety of aquatic systems.

B. Develop a predictive model based on nitrogen loading for systems limited by nitrogen.

C. Study the quantitative role of biota in nutrient cycling, particularly transformations, algal uptake and release, macrophyte pumping of nutrients, zooplankton assimilation and excretion, and cycling of nutrients by fishes.

D. Improve methods for distinguishing between nutrient forms to determine availability to biota and to measure flux between forms.

E. Study the indirect effects of nutrients on higher trophic levels.

F. Evaluate the direct effects of nutrient additions on macrophytes and periphyton.

G. Investigate the significance of nitrogen stimulation of decomposition to system productivity.

H. Research the role of nutrients in streams and reservoirs.

3.8 NUTRIENT-SEDIMENT INTERACTIONS

A. Obtain more data on nutrient-nutrient and sediment-nutrient interactions, since various nutrient combinations may act synergistically when added to a waterbody and nutrients carried by sediment may stimulate productivity.

B. Quantify nutrients in bottom sediments and determine their availability.

CHAPTER 4

ORGANIZING CONCEPTS AND DEFINITIONS

4.1 INTRODUCTION

Most research on impacts in aquatic systems has followed a fragmentary or component analysis of effects. This methodology is not completely satisfactory because aquatic communities are ecological systems that are dynamically interactive between components of the communities and between communities. There is a need to conceptualize and to investigate aquatic systems holistically by considering the interactive nature of their physical, chemical, and biological properties and by organizing the systems hierarchically. This chapter discusses properties and behavior of ecosystems, shows the need for and limitations of aquatic classification methodologies, and develops the organizational scheme for the study.

4.2 ECOSYSTEM APPROACH

A central organizational scheme that has guided this study is based on the ecological system or ecosystem. An ecosystem is composed of living organisms, i.e., a biota, interacting with other organisms and with the physicochemical environment to create a recognizable and coherent ensemble (Odum 1953). A lake or a forested watershed is an example of an ecological system.

We have expanded this ecosystem concept to provide a hierarchy of ecosystems as was proposed by Evans (1956). Francis Evans pointed out that if ecosystem is defined as a system composed of interacting biotic and abiotic subsystems, then ecosystems can exist at a variety of levels. That is, an individual plus its environment forms an ecosystem; a population plus its environment forms an ecosystem; a community plus its environment forms an ecosystem; a watershed and its environment forms an ecosystem, and, indeed, the entire United States and its environment also forms an ecosystem. This approach is broader than that of Odum's (1953 and later editions) and the more usual view which restricts the use of ecosystem to the biological community and its environment.

Since an ecosystem is defined as a system or entity, it is assumed that ecosystems have limits and can be distinguished from one another. However, the problem of specifying the boundaries of an ecosystem often is difficult since some organisms are wide ranging, others are sedentary, the physicochemical environment often is continuous, and both the living and nonliving complexes change over time. Frequently boundaries can be recognized and used to identify and separate ecosystems. For example, the margin of a lake or the water divide of the watershed is recognized easily. But, more often, boundaries are diffuse and occupy substantial space. In those cases the system limits are defined arbitrarily on the basis of study objectives.

Materials and energy in physical, chemical, and biological form flow across system boundaries. The behavior of an ecosystem is described by its qualitative and quantitative methods of processing inputs of materials and energy into outputs. For example, inputs of solar energy might be converted into outputs of heat and organic materials. These organic materials may serve as inputs to other ecosystems, linked to the one under discussion, while the heat is moved from the hydrosphere to the atmosphere and creates a warmer or cooler microclimate in neighboring systems.

The relation of inputs to outputs and the system behavior is seldom constant. Rather, behavior oscillates over time responding to changes in the environment or to shifts within the system components. However, often the trajectory of system behavior can be predicted, and we can identify a stability zone within which the behavior is expected to lie. Clearly, one of our problems is to identify those stability levels and then determine how various impacts change the level of system behavior.

To explain this behavior requires analysis of the structure and function of the ecological system (see Chapter 6). This is difficult because so many different types of subsystems might be recognized. For example, disaggregation of a lake or river ecosystem into its constituent species populations could require hundreds, if not thousands, of coupled subsystems. It is important that we only recognize those subsystems that explain the system behavior because our analytical tools are limited, while the diversity of nature is very large. This is a very creative and controversial step in ecosystem study.

Identification of the subsystems specifies the structure of the ecological system. Structure might be expressed as mass, energy, chemical elements or compounds, species, groups of species, and so on. The next step in the explanation of ecosystem behavior involves study of the interaction of the subsystems, or, in other words, study of their function. For example, this could involve the flow of energy or materials between subsystems through feeding activity. These functional studies, analogous to the study of the physiology of the individual, are a key step in the analysis. They are difficult, especially in natural systems, since controlled experiments can seldom be carried out. Further, to be useful for our purposes, the functional studies must be tied back to an explanation of the overall system behavior. However, information obtained from the measurement of functional variables is necessary to the understanding of dynamic behavior in aquatic systems.

In most instances there are environmental systems outside of the biotic subsystems or outside the ecosystem itself which can impact the system and alter its behavior. Typically these environmental impacts operate on subsystems, altering the subsystem interactions and flows of energy and materials. These subsystem effects, in turn, alter the overall system behavior. That is, at certain levels of impact or input, the system response is positive. However, at other levels the response is negative. In a simple case the effects of an impact can be described by a performance curve (Fig. 4.1). Management focuses on maintaining the system behavior at certain points of the performance curves. Ideally, we should have families of performance curves for all significant ecosystems, ecosystem components, and all important migrating phenomena.

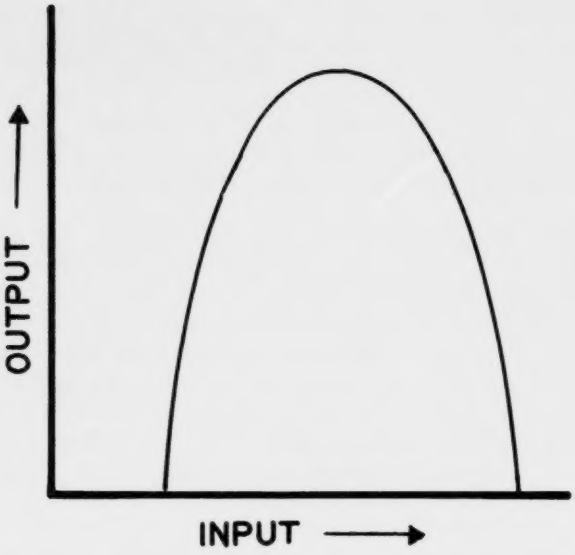

Fig. 4.1. An example of a performance curve.

Models are an important tool for describing ecosystem structure and function and they also may be used to predict system response to impacts. Many types of aquatic models exist (see Chapter 7). Some are general and may be applied to several system types while others are more specific to a particular system. Macroscopic properties may be considered or the emphasis may be on component variables and interactions. The degree to which terrestrial influences are included varies as well as does consideration of temporal changes. The choice of a model will depend upon the particular system studied, the questions being asked, and whether a macroscopic or finer resolution view is taken.

4.3 AQUATIC SYSTEM CLASSIFICATION

A classification is needed which categorizes aquatic ecosystems by sediment and nutrient concentrations and by their responses to sediment and nutrient loading. The major problem is selecting a level of classification which is manageable, i.e., having a small number of categories, yet permitting enough resolution to detect differences in biotic responses. The scheme would ideally group streams, rivers, lakes, and reservoirs by a type of measurable response given to a known sediment or nutrient input.

Three types of measurements can be incorporated into a classification system for aquatic ecosystems--physical, chemical, and biological. Physical characteristics may include channel morphology, substrate type, current velocity, seasonal changes in flow rates, basin depth and width, sediment, turbidity, etc. Chemical parameters may include dissolved oxygen, nutrients, salts, conductivity, and concentrations of various chemicals. Common biological measurements consist of species composition, richness and diversity, numbers of organisms, biomass, productivity, and respiration. The extent to which any of these categories is included in a classification system depends on the specific requirements of the user, economic feasibility, and the hierarchical level studied. Biological sampling often is very time consuming and is, therefore, expensive--as is the determination of many trace chemical compounds. Table 4.1 lists some of the advantages and disadvantages of using physicochemical or biological measurements for classifying aquatic systems.

The initial attempt in this study to organize aquatic ecosystems was based on a "component" approach. Aquatic ecosystems were divided into lentic (standing) and lotic (flowing) habitats, with subsequent division based on various physical, chemical, and biological parameters. Lotic waters were examined first. Stream classifications from federal and state agencies generally are management oriented and depend on only a few water quality parameters such as dissolved oxygen, pH, turbidity, and/or channel morphology. Other schemes which employ multiple characters result in a vast number of "classes." Using Pennak's (1971) system which incorporates stream width, current, substrate, maximum and minimum temperature, turbidity, dissolved organic and inorganic content, hardness, measures of pollution, rooted aquatic cover, and stream side cover, there could be 184,320,000 classes of streams--considerably more classes than there are streams. Stream classifications based on biological criteria mostly depend on identification of distinct floral or faunal indicator species or communities. Unfortunately, biological species overlap greatly with adjacent communities, thereby introducing a potentially large error in the classification system.

Given these problems, Pennak's system was modified by reducing the number of parameters and levels so that a manageable number of classes resulted. Three parameters were selected initially: temperature, sediment concentration, and channel gradient (slope). Each parameter was then divided so that two classes could be derived from each parameter, one above and one below each division. The divisions were temperature = 24° C, sediment concentration = 220 ppm, and gradient = 4 percent. The rationale for choosing these parameters and divisions was based on their correlation with other parameters. Specifically, temperature directly affects dissolved oxygen and determines the distribution of a number of aquatic organisms. The temperature division at 24° is based on the separation at that temperature of warm and cold water fisheries. Sediment concentration was divided at 220 ppm because of a previous mapping division (Rainwater 1966) and the possible suggestion that impacts on aquatic organisms would probably be minor below this level. Channel gradient determines current velocity and hence substrate type (mud, silt, gravel, rock, etc.). A gradient of 4 percent is the approximate division between a sand or gravel bottom based on the distribution of warm and cold water fisheries. Nutrient levels were not considered since streams are generally detrital based systems which do not respond to nutrient additions; only in some reaches or in

Table 4.1 Advantages and disadvantages of classifying aquatic ecosystems by physico-chemical and biological parameters.

I. Physico-chemical
  a. Advantages
    1. "Hard" data at detailed level
    2. Ease of measurement (except for trace chemical compounds)
    3. Probably high correlation with biological communities
    4. Specific identification of environmental changes
    5. Comparisons between streams across geographical and temporal scales
  b. Disadvantages
    1. Indirect measurement of biota
    2. Potentially large number of aquatic classes
    3. Large data base necessary to permit biological correlations
    4. Variability subject to designation of each parameter's breakdown into subunits (e.g., temperature ranges or current velocity)
    5. Expense of data acquisition and analysis

II. Biological
  a. Advantages
    1. Direct assessment of flora and fauna
    2. Detection of minor shifts in community structure
    3. Some organisms extremely sensitive to trace amounts of chemicals in systems
    4. Effects over time period instead of sampling-time conditions
  b. Disadvantages
    1. Large sample size needed for statistical analysis
    2. High variance between aquatic systems
    3. Sample collecting and processing expensive and time consuming
    4. Observed changes may not be due to sediment or nutrients or may be synergistic effects of more than one factor (difficult to discover specific causative agent)
    5. Overlap zone areas of same aquatic system can be large
    6. Comparisons across geographic and temporal gradients are valid only when used in a general sense
    7. Ubiquitous organisms often not sensitive to change

streams of a particular size may nutrients stimulate primary production.

This classification scheme was expected to partition the different parts of the country by differences in biotic responses to sediment loading in streams. Initial coarse mapping showed distinct partitioning. The scheme could be tested by assembling the results of all sediment related impact studies and placing each study's location on the map. If valid, differences in biological responses between regions should be evident. Validation of this classification system in physico-chemical terms was attempted by using data from various water quality stations throughout the country. Data from the STORET system were used, but the scheme could not be validated by this data source. The data had different units, stations lacked measurements for all three parameters, subroutines to retrieve data were not available, and cost to solve problems was beyond the budget of this project. Also, biological data were lacking, hence meaningful regional interpretations were not possible.

Lentic waters presented a different problem. A review of the literature revealed that nutrient conditions in lakes, i.e., the initial nutrient state, influenced the impacts of nutrient loading but that impacts by sediment were generally less important. Therefore, a classification system based on trophic state was adopted. This scheme relies on several important indicators of water quality including a measure of primary productivity, turbidity, and major nutrient concentrations. Three major categories result ranging from relatively pristine water to polluted waters--oligotrophic, mesotrophic, and eutrophic. (In this report these groups are always referred to as trophic states or categories and should not be confused with trophic levels. Trophic level is used to denote the position in the food chain, i.e., producer, herbivore, carnivore.) However, this view required examination of each water body not only for the trophic state but also for other variables which might influence system response. In the component approach waters were artificially divided into flowing and standing waters. Sediment and nutrient inputs were also separated by system type, although they might have an influence in any system type and have been shown to interact with each other. The component approach was, therefore, expanded to a hierarchical ecosystem approach which includes streams, rivers, lakes, and reservoirs, and which considers the impacts of both sediment and nutrients in any water body.

4.4 HIERARCHICAL ECOSYSTEM APPROACH

It has become well recognized in recent years that aquatic ecosystems reflect the terrestrial ecosystems to which they are linked (Likens and Borman 1974; Sioli 1975) and that any classification of aquatic systems also must include features of the terrestrial environment. A classification of standing and running water that reflects the interaction of climate, soil, vegetation, geomorphology, and land use, as well as the character of the waters, is needed. This system should emphasize the geographical as well as the biological features of aquatic systems in developing a hierarchy of ecological systems.

Applying the concept of ecosystem in the sense of Evans (1956) and the method of ecosystem analysis described earlier, we can develop a variety of system hierarchies. For example, beginning with the ecosphere, i.e., the biosphere plus the atmosphere, lithosphere, and hydrosphere forms a nested set or hierarchy (Table 4.2). Of course, a variety of hierarchies can be recognized depending upon one's objectives and point of view (MacMahon et al. 1978).

Table 4.2. A selected set of biological and ecological entities forming an ecological hierarchy. An ecosystem is defined as a biotic complex interacting with its biological, physical, and chemical environment (Odum 1953; Evans 1966).

Biological Units		Environment		Ecological Systems	Level	Number of Units
Biosphere	+	Hydrosphere Lithosphere Atmosphere	=	Ecosphere	1	1
Nation	+	Environment	=	Nation Ecosystem	2	1
Region(s)	+	Environment	=	Region Ecosystem	3	24
Watershed	+	Environment	=	Watershed Ecosystem	4	≥1200
Community	+	Environment	=	Community Ecosystem	5	?
Population	+	Environment	=	Population Ecosystem	6	?
Individual	+	Environment	=	Individual Ecosystem	7	?

The hierarchical system integrates climatological, geological, topographic, vegetative, and aquatic factors (physical, chemical, and biological) affecting sediment and nutrient impacts throughout the United States. The rationale for using a geographical approach is based on several factors. Such an approach is supported by literature showing climatic, hydrological, soil, and vegetational similarities. The approach is consistent with the broad concept of ecosystem. An ecosystem classification based on geographical criteria integrates all aspects of the project into a single scheme. The scheme allows mapping of similar factors, and in complex areas variables can be examined at subregional levels for finer resolution. Geographical regions can be defined independent of specific levels of sediment or nutrients. Then these levels can be compared from region to region (see Chapter 5).

In contrast, at the finer levels of the hierarchy (levels 4 - 7) physical factors are still important but aquatic systems and organisms become the focus. Then we must utilize the schemes of classification of aquatic habitats by limnologists and ecologists, including the separation of freshwaters into lentic or lotic systems and the use of trophic state. Having identified the appropriate ecological components to be quantified in assessing impacts at each level of resolution (see Chapter 6), the roles of sediment, phosphorus, and nitrogen are examined in Chapters 9 and 10. The physical and chemical factors which most affect the nature of impact for each substance also are identified (e.g., water depth, temperature, turbidity, waterflow, volume, etc.). By organizing the characteristics of the various ecosystems in a hierarchical manner, the most appropriate measure of biotic response and the importance of controlling physical factors can be determined more easily.

The lower levels of organization which are most frequently researched have created a bias in this report. Study of large aquatic ecosystems, as ecosystems, is relatively recent. Study of the hydrology and the biology of freshwater organisms is older, and much more information in available. Therefore, more material is included for finer levels of the hierarchy than for the larger systems.

The idea of a hierarchy of freshwater ecosystems underlies this entire report. A set called freshwater ecosystems of the United States can be visualized. This set includes about 1200 major river basins (watersheds) and 500 large lakes and impoundments. The United States government must manage this set as a whole. While regulations might be tailored to specific freshwater systems, federal agencies probably cannot manage at lower levels of biological organization or for every reach of a stream. For example, it might be possible to develop special regulations for different river basins, but specific communities within the basin cannot be treated individually. Indeed, this might be a central problem in water management in the United States. Therefore, the surface waters of the United States are the first level of our hierarchy. What is true of all United States freshwaters? Can general statements and regulations for all freshwaters be made. These questions are addressed in this report.

As far as we know, no one has taken a hierarchical approach to freshwater ecology, and, yet, we suspect that it is an essential viewpoint for management of the aquatic environment of the nation. Thus, the goal of the study might be rephrased. The objective is to determine how an integrated, holistic plan of water management might be organized and what research is required to implement this type of ecological management of the nation's waters.

Summarizing, the study of the impact of nutrients and sediment on the biota of the nation's freshwaters is complex and exceedingly broad. We have assumed that the problem can best be approached from an ecosystem hierarchical point of view, since it allows organization and analysis of information on a variety of geographical and biological scales.

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CHAPTER 5

DEVELOPMENT OF A REGIONAL ANALYSIS OF FRESHWATER ECOSYSTEMS

5.1 INTRODUCTION

The degree to which freshwater ecosystems are affected by sediment and nutrient loading and concentrations is determined by many biotic and abiotic factors. Physiography, geology soil type, vegetation, climate and man's activities affect these biotic and abiotic factors and show regional distributions. Generally, aquatic ecosystems within a given region should be more homogeneous with respect to environmental criteria used to define that region than aquatic systems in other regions. Therefore, the division of surface waters into regions is valid. This division allows comparison of sediment and nutrient loading and concentration between different parts of the country and organizes existing information on impacts of sediment and nutrients on biota in surface waters. This regional organizing scheme also indicates where additional information is needed on water characteristics and on impacts of biota.

The hierarchical scheme proposed in Table 4.2 shows that levels 1 - 3, the biosphere, nation, and region, are geographical in nature. Since management of the waters of the United States is the goal, the "regional" level of the hierarchy is an appropriate starting point at which to develop the analysis of similarities and differences in aquatic systems throughout the nation. Analysis at this level will help to determine if there are distinct areas of the country that have water characteristics which would affect the nature of impacts on biota. A regional approach is appropriate for this study because 1) it is supported by literature showing regional climatic, soil, and vegetational similarities; 2) it is consistent with the broad concept of ecosystem, the integrative principle of all aspects of this project; and 3) it allows mapping of similar factors.

In this chapter an eco-geographical scheme at the "regional" level is described. The scheme is used to show the distribution of sediment and nutrient concentration in surface waters and to show the interactions of sediment, phosphorus, nitrogen, land use, and salinity.

5.2 GEOGRAPHICAL CLASSIFICATION SYSTEMS

Regional studies have been used in geography for many years to divide the world into areas based on climate, topography, and vegetation. These attempts usually have been based on distribution of climatic-vegetational zones rather than animal-community distribution. Merriam's (1898) life zone hypothesis and Dice's (1943) biotic province scheme are examples of regional ecological classification systems. The climatic classification of Thornthwaite (1931) and physiographic regionalization of Fenneman (1928) have been widely used by geographers and ecologists.

Vegetation is used in most ecological regional definitions because vegetation combines environmental effects of climate, soils, and topography. Clements and Shelford (1939) devised a scheme in which climax vegetation and its associated faunal groups were organized into biomes. Biogeographical provinces based on major biomes or on biome complexes geographically dominating a region have been mapped by Dasmann (1972) and by Udvardy (1975). Other regional schemes have been developed by Crowley (1967), Wertz and Arnold (1972), Lacate (1969), Hills (1952, 1960), Burger (1976), Rowe (1972), and Hodgkins (1965) to show land groupings and ecological regions within areas of North America. These schemes are based to different degrees on land form, lithology, relief, climate, soils, and vegetation (Bailey et al. 1979). Küchler (1964) proposed a scheme for stratifying and evaluating land potential for vegetative production on a national scale and provided a map and a manual describing his concepts for broad planning of land and natural resources.

Attempts by the federal government to inventory and study individual natural resources of the United States beginning in the 1930s and continuing through the 1950s were inadequate because classification was based upon the individual resources themselves. There was no uniform integrative classification system that was based upon natural ecosystem properties (Baily et al. 1979). Recent approaches to land and natural resource classification have expanded to provide information on physical features, distribution of the resources, and the nature of interactions of the physical features, resources, and land use practices. Habitat hierarchies have been developed so that land units with similar characteristics can be grouped and generalizations about larger groupings can be made. The soil taxonomy classification is an example of such hierarchical organization (Soil Survey Staff 1975).

Robert G. Bailey (1976, 1977) has proposed an integrated scheme that attempts to define ecological regions (ecoregions) of the United States. Bailey's "Ecoregions of the United States" appears to be the best available method to organize the existing information on regionalization of environmental/ecological factors for the purposes of this study. Bailey's scheme integrates other regional schemes into a functional system that has a broad use for a variety of purposes. This classification system has been adopted by at least nine federal agencies and 12 private groups for inventories, land use planning and assessments, and impact analyses (Bailey, personal communication). The scheme has the potential to integrate ecological research and management of resources. This system currently appears to be the best method available for showing the interactions of terrestrial and aquatic systems and, therefore, has been adopted for the development of a hierarchy of aquatic ecosystems of the United States.

Bailey's ecoregion classification, derived from Crowley (1967) and Wertz and Arnold (1972), divides the United States into hierarchical classes. The system is based upon the need to develop a classification scheme that would encompass the entire country, that would be objective, ecologically sound, and be useful to land managers at any level of hierarchical organization. Bailey states that the regional view of ecosystems is needed 1) to permit detailed data to be aggregated into more generalized units for decision-making at higher levels, and 2) to provide an integrating frame of reference to interpret fully more detailed information. Bailey considers ecoregions to be distinct geographical areas having distinctive flora, fauna, climate, land form, soil, vegetation, and ecological climax.

The classification scheme used by Bailey has nine levels of organization, but only the three upper levels are used in this report, i.e., Domain, Division, and Province.

1. Domain - A subcontinental area of broad, climatic similarity (Fig. 5.1).
2. Division - A subdivision of the "Domain" determined by isolating areas of different vegetation and regional climates, generally at the level of the basic climatic types of Köppen (Fig. 5.2).
3. Province - A subdivision of the "Division" that corresponds to a broad vegetation region having uniform regional climate and the same type or types of zonal soils (Fig. 5.3).

Generally each province is characterized by a single vegetation climax association although two or more climaxes are sometimes represented within a single province, e.g., in the mountains where altitudinal zonation results in a complex of vegetation. These provinces are not easily separated because middle and upper slopes of mountain regions have different climates from adjacent lowlands.

The province level of regionalization was adopted for our analysis, because it integrates climate, soils, and vegetation on a broad, regional basis, and provides a manageable number of units. The Province level provides the best opportunity to show similarities and differences in sediment and nutrients in surface water and to categorize impacts from these parameters. Lower levels of the Bailey scheme are too numerous and dissected to provide a broad, regional interpretation. Features of lower levels are aggregated in the Province category.

5.3 METHODS FOR CHARACTERIZING ECOREGIONS

Data in mapped form were available for concentrations of nitrogen, phosphorus, and sediment, and for hardness of surface waters. Trends in concentrations of nitrogen, phosphorus, sediment, and hardness in the surface waters of the Bailey provinces of the United States were determined by using these data and through modification of these maps by mapping overlay techniques. The percent of waters having different concentration levels was calculated for each province and are displayed as histograms; differences in land use, as the percent of land use categories in each province are also shown (Fig. 5.4 - 5.27).

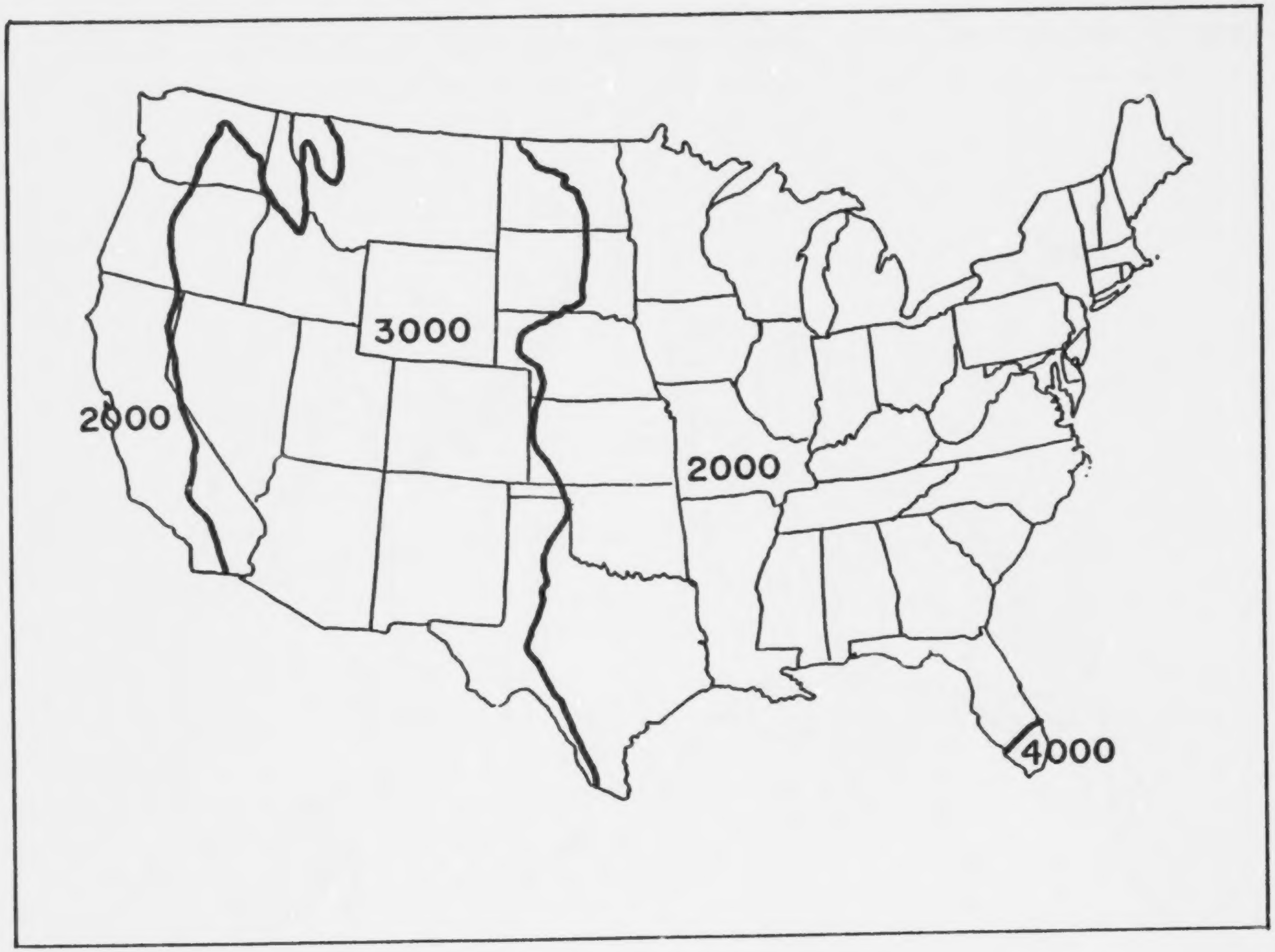

3000
2000
2000
4000

Fig. 5.1. Domains of the Bailey Ecoregion Classification Scheme. (2000 - Humid Temperate; 3000 - Dry; 4000 - Humid Tropical)

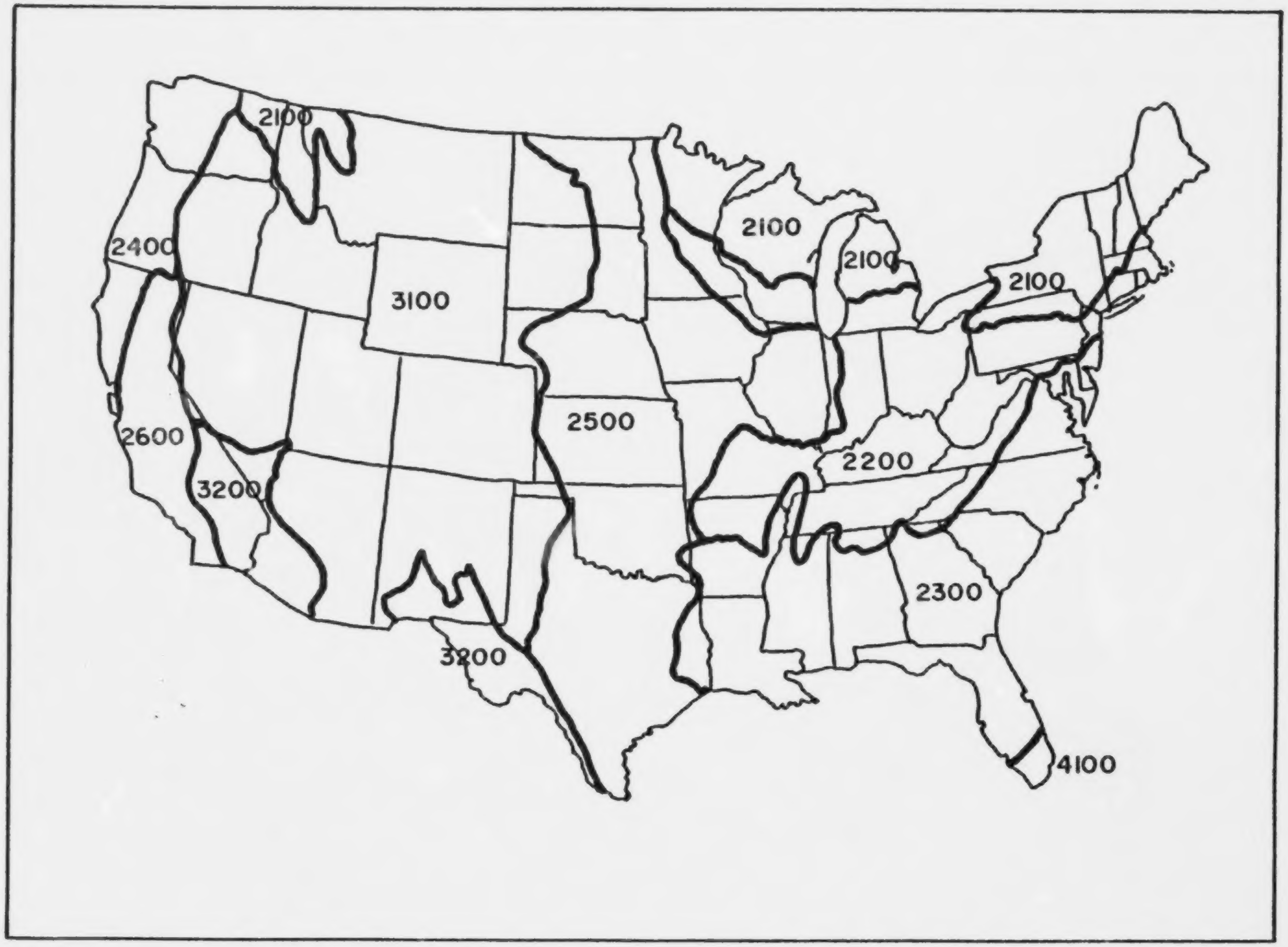

2100
2400
3100
2100
2100
2100
2600
2500
2200
3200
3200
2300
4100

Fig. 5.2. Divisions of the Bailey Ecoregion Classification Scheme. (2100 - Warm Continental; 2200 - Hot Continental; 2300 - Subtropical; 2400 - Marine; 2500 - Prairie; 2600 - Mediterranean; 3100 - Steppe; 3200 - Desert; 4100 - Savannah)

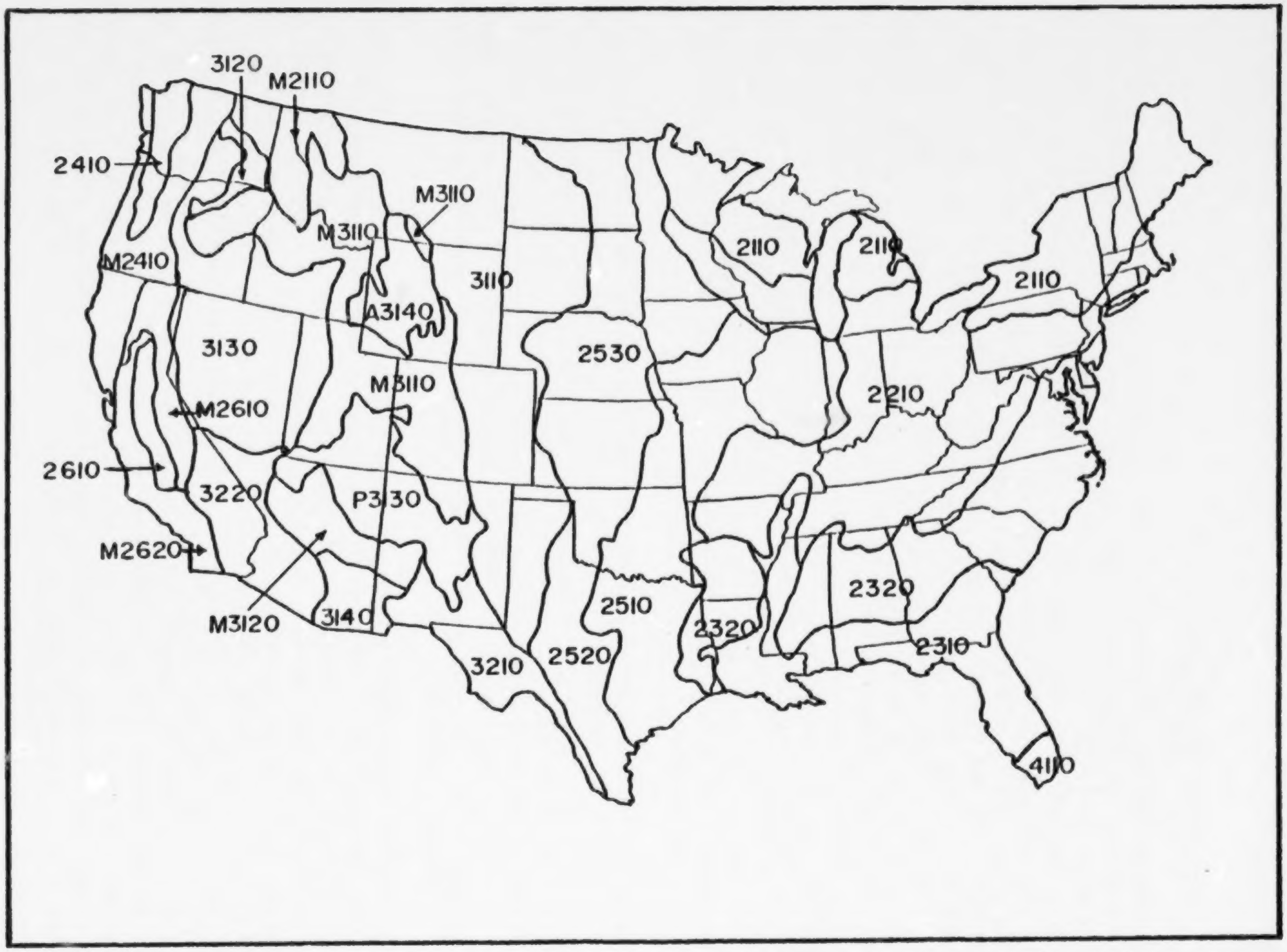

3120
M2110
2410
M3110
M3110
M2410
2110
2110
2110
3110
A3140
3130
2530
M3110
2210
M2610
2610
3220
P3130
M2620
2320
2510
2320
M3120
3140
2310
3210
2520
4110

Fig. 5.3. Provinces of the Bailey Ecoregion Classification Scheme. Provinces designated here by numbers are named in section 5.4.

Data for other nutrients, e.g., carbon, was not available readily and, hence, was not used. Since nitrogen, phosphorus, and sediment impacts are reviewed in Chapters 9 and 10, it is appropriate to characterize them in the regional scheme.

5.3.1 Nitrogen and Phosphorus

Nitrogen and phosphorus concentrations were derived from maps prepared by Omernik (1977a, 1977b) showing total nitrogen and total phosphorus in streams. The data were collected from 928 stream sites throughout the United States in watersheds having only non-point source inputs. Streams were sampled at least monthly for one year during the 1972 - 1975 National Eutrophication Survey. The concentrations of nitrogen and phosphorus have low reliability in the Southeastern Coastal Plain, including all of Florida, the Great Basin, and the Southwestern Deserts because these areas were not sampled adequately during the survey. However, these stream data were used because they were the best available, were in a mapped form, and because accessible nitrogen and phosphorus data on lakes and reservoirs were lacking. Stream data are adequate to categorize the broad differences in nitrogen and phosphorus concentrations, but are not necessarily representative of lake or reservoir conditions. Lakes and reservoirs would be expected to show qualitative similarities to rivers because of terrestrial/aquatic interaction. Point source loadings alter drastically these qualitative correlations. Stream data probably underestimate nitrogen and phosphorus levels in lakes and reservoirs because of flushing of these nutrients from streams.

Omernik's 10 concentration classes were aggregated into three classes to represent levels of phosphorus and nitrogen that generally are associated with oligo-, meso-, and eutrophic water conditions (Wetzel 1975). Concentration classes for nitrogen are less than 0.9, 0.9 to 2.0, and greater than 2.0 mg/l. Concentration classes for phosphorus are less than 0.005, 0.005 to 0.030, and greater than 0.030 mg/l total P. These classes were designated as low, medium, and high concentrations in the subsequent discussion of phosphorus and nitrogen in the different provinces.

Subsequent comparison of provinces was based on the percent of streams in a province having certain concentration ranges of nitrogen and phosphorus. For example, nitrogen or phosphorus concentrations for rivers in provinces may have been distributed in low, medium, and high categories. In order to establish the general trend in distribution of concentrations for a province and to easily compare provinces, further categorization was necessary. A province with greater than 70 percent of the streams having low concentrations was designated as a "Low" region; greater than 70 percent in the medium class, a "Medium" region; greater than 70 percent in the high class, a "High" region; 40 to 60 percent in the medium class and the rest predominantly in the low class, a "Medium-Low" region. Similar provinces, e.g., three provinces with 70 percent of the streams having low concentrations, were designated on the maps of the provinces (Fig. 5.28, 5.29) and exhibited in tabular form (Table 5.1).

5.3.2 Sediment

Sedimentation concentration of rivers throughout the United States was taken from information mapped by F. H. Rainwater (1966). Seven concentration classes of sediment were established in rivers throughout the United States as annual load divided by annual streamflow. These have been aggregated into three classes--less than 270, 270 to 1900, and greater than 1900 ppm which are referred to as low, medium, and high concentrations. These classes were chosen because they were levels mapped by Rainwater and because they represent reasonable categories in terms of suspected impact levels. Concentrations of sediment in each province were presented as histograms indicating the percentage of those streams in an area showing a particular concentration class. Subsequent mapping of these concentrations was done to determine provinces with similar sediment characteristics as described above for nitrogen and phosphorus. Sediment categories are designated as High, Medium High, Medium Low, and Low and are presented in tabular and mapped form (Fig. 5.30 and Table 5.1).

5.3.3 Land Use

Land use alters inputs of sediment and nutrients into aquatic systems. Streams draining agricultural watersheds have higher nutrient concentrations than those draining forested watersheds. Total phosphorus is approximately ten times greater and total nitrogen approximately five times greater in streams draining agricultural watersheds (Omernik 1976). Data to determine percent of land use in a province were derived from an unpublished report to EPA titled, "National Assessment of Water Pollution from Non-Point Sources - Appendix" (Midwest Research Institute 1975). Land use was presented for major and minor river basins throughout the United States. The percent of land area in various land use categories for each province in the United States was determined by overlaying province boundaries on river basin boundaries, establishing from this the river basins involved, and then extracting the land use data from minor river basins from the report. Province boundaries frequently did not coincide with river basin boundaries, hence, best estimates and proportions were used to arrive at the final land use acreage.

Only agricultural (including range) and forested areas and, to a minor extent, urban areas represent significant land uses at the province level of this regional classification scheme. Urban areas, generally not more than 1 - 2 percent of a province area, can contribute significant inputs of nutrients and sediment during runoff. Construction and mining contribute sediment to localized areas but are not major contributing factors over the large land area, the province, used in this classification scheme.

Land uses were plotted initially as histograms showing the percent of forested, agricultural, and urban use in each province. Subsequent mapping to show similarities in land use between provinces employed only agricultural and forested land (Fig. 5.31). Relative percentages of agricultural and forested use were divided for province similarity comparison as; greater than 70 percent agricultural, greater than 70 percent forest, 50 percent forested/ 50 percent agricultural, 60 percent agricultural/40 percent forested, and 60 percent forested/40 percent agricultural.

5.3.4 Hardness

Water hardness may modify sediment and nutrient impacts and may result in differences in species composition at different hardness levels. Therefore, we have incorporated differences in hardness to show trends in soft and hard water throughout the nation and to identify areas where hardness should be considered in impact evaluation.

Hardness of surface water throughout the United States was determined from data mapped in the "Water Atlas of the United States" (Geraghty et al. 1973). Five levels of $CaCO_3$ were mapped for the rivers of the nation--less than 60, 60 - 120, 120 - 180, 180 - 240, and greater than 240 ppm. Concentrations below 60 ppm were considered soft, 60 - 120 ppm medium-hard, and greater than 120 ppm hard. These concentration categories were plotted as histograms to reflect the percent of the rivers in a province with a given concentration of $CaCO_3$. The relative percentages of the high (hard), medium, and low (soft) hardness categories in each province were converted to Low, Medium, High, Medium Low, and Medium High categories based on the criteria used for nitrogen and phosphorus. These categories were compared by province and were tabulated and plotted to show similarities in hardness between provinces (Fig. 5.32).

Further comparisons were mapped to show provinces that have rivers with similarities in concentrations of nitrogen and phosphorus, and sediment; land use and sediment; land use and phosphorus; and land use and nitrogen (Fig. 5.33-5.39).

5.4 CHARACTERIZATION OF THE ECOREGIONS - DOMAINS, DIVISIONS, AND PROVINCES

The use of Bailey's ecoregion scheme to account for variability in impacts of sediment and nutrients on biota assumes that physical and chemical characteristics peculiar to different areas of the United States are distributed approximately according to Bailey's ecoregions. Bailey's third level of ecological regionalization, "Province," has been selected to show regional variations in physical and chemical parameters. The Domain, Division, and Province descriptions are presented here to provide a context for analysis of the nitrogen, phosphorus, sediment, land use, and hardness information.

Domain 2000 - HUMID TEMPERATE

This domain comprises the humid mid-latitude broadleaf and coniferous forest of the eastern United States and the Pacific Coast.

Division 2100 - WARM CONTINENTAL

This division is characterized by very cold winters and warm summers. Maximum stream flow, occurring in the spring, is associated with snow melt and rain. A slight summer minimum is found.

Province 2110 - Laurentian Mixed Forest (Fig. 5.4)

Province M2110 - Columbia Forest (Fig. 5.5)

Division 2200 - HOT CONTINENTAL

Division 2200 has cold winters and hot summers. Maximum stream flow occurs in the spring and is associated partially with snow melt and rain. The main winter flow is only slightly greater than the summer minimum.

Province 2210 - Eastern Deciduous Forest (Fig. 5.6)

Division 2300 - SUBTROPICAL

Mild winters and hot summers characterize the subtropical Division. Streams flow all year with a spring maximum and a winter minimum. Maximum runoff occurs in April or May and minimum runoff in August or September. The southern portion of the division has high summer rainfall resulting in warm-season flow exceeding winter flow. The northern portion rainfall pattern is the reverse of the southern area.

Province 2310 - Outer Coastal Plain (Fig. 5.7)

Province 2320 - Southeastern Mixed Forest (Fig. 5.8)

Division 2400 - MARINE

The Marine Division has mild winters with little frost and cool summers. Streams flow year round with a slight warm season minimum in late summer and early autumn.

Province 2410 - Willamette-Puget Forest (Fig. 5.9)

Province M2410 - Pacific Forest (Fig. 5.10)

Division 2500 - PRAIRIE

The Prairie Division has a variable and subhumid climate. Stream flow is maximum in summer and minimum in winter with secondary maximum flow in the spring from snow melt.

Province 2510 - Prairie Parkland (Fig. 5.11)

Province 2520 - Prairie Brushland (Fig. 5.12)

Province 2530 - Tall Grass Prairie (Fig. 5.13)

Division 2600 - MEDITERRANEAN

This area of central and southern California has dry summers and mild winters. Minimum stream flow occurs in summer due to intense surface insolation and minimal precipitation. Some snow melt in the spring increases flow. High flows are found in other seasons from heavy precipitation associated with moist westerly air flow.

Province 2610 - California Grassland (Fig. 5.14)

Province M2610 - Sierran Forest (Fig. 5.15)

Province M2620 - California Chaparral (Fig. 5.16)

Domain 3000 - DRY

This domain encompasses the arid and semi-arid regions of the country and has discontinuous steppe, xerophytic bush, and desert vegetation.

Division 3100 - STEPPE

The Steppe area has a semi-arid climate with a dry season, which may extend 8 - 9 months, and cold winters. Potential evaporation exceeds precipitation resulting in no water surplus. Summer maximum stream flow with flooding from snow melt, localized flooding from high intensity summer storms, and low flows in fall and winter typify the hydrology of the area.

Province 3110 - Great Plains Short Grass Prairie (Fig. 5.17)

Province M3110 - Rocky Mountain Forest (Fig. 5.18)

Province 3120 - Palouse Grassland (Fig. 5.19)

Province M3120 - Upper Gila Mountain Forest (Fig. 5.20)

Province 3130 - Intermountain Sagebrush (Fig. 5.21)

Province P3130 - Colorado Plateau (Fig. 5.22)

Province 3140 - Mexican Highlands Shrub Steppe (Fig. 5.23)

Province A3140 - Wyoming Basin (Fig. 5.24)

Domain 4000 - HUMID TROPICAL

This domain is found in extreme southern Florida and has persistently high moisture and temperature.

Division 4100 - SAVANNAH

> The Savannah Division has a tropical wet/dry climate with the wet season controlled by moist, warm, maritime tropical air masses and dry season controlled by continental tropical air masses. Stream flow is maximum in the summer with extended low water periods in winter and late spring.

The following is a brief characterization of the Provinces in terms of geographical location, mean annual temperature and precipitation, vegetation, and soils. Nitrogen, phosphorus, and sediment concentrations in streams, land use, and water hardness derived from analysis of stream and land characteristics are presented.

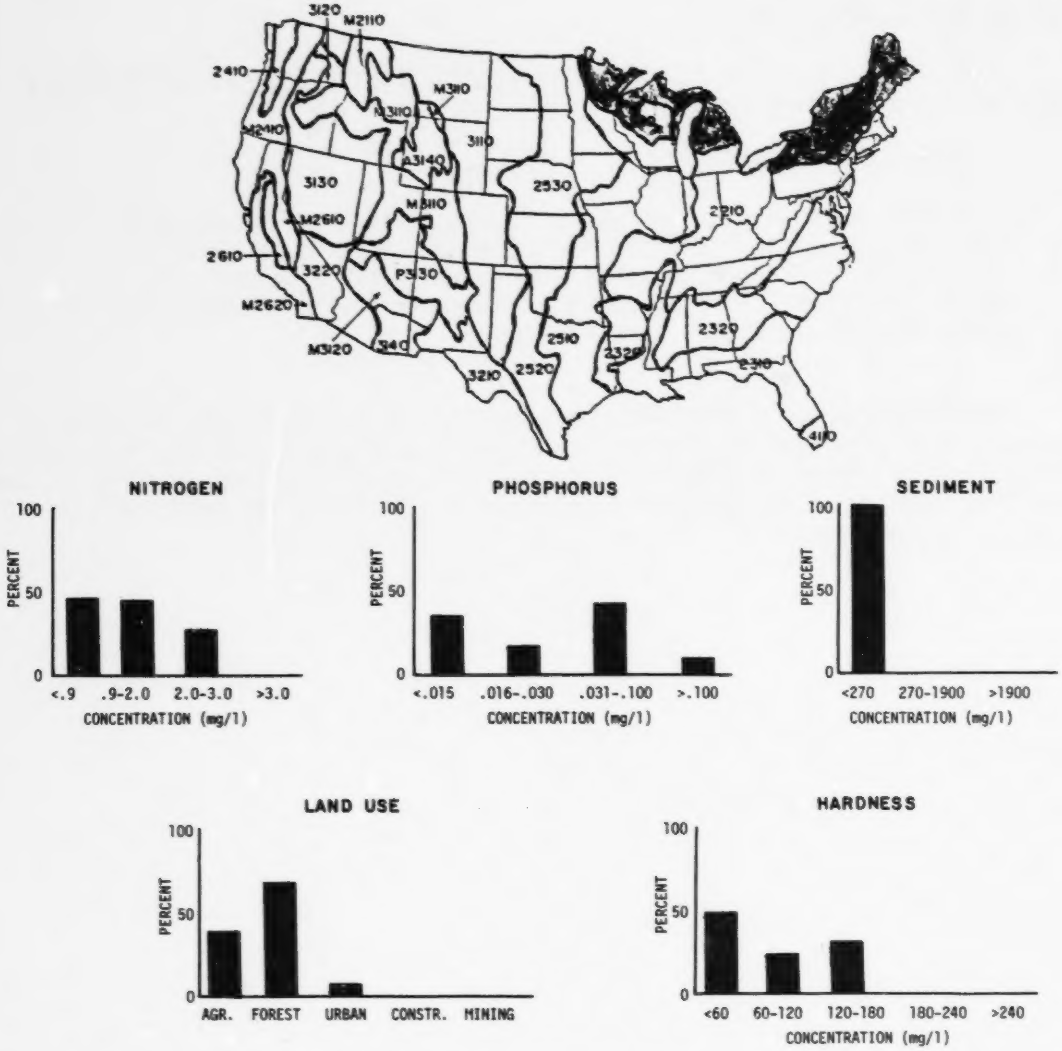


Fig. 5.4. Province 2110 - LAURENTIAN MIXED FOREST

The Laurentian Mixed Forest encompasses an area of 24,700 mi^2 in the Northeast and Great Lakes region of northern Wisconsin, Minnesota, and Michigan. The average annual temperature is 2-10° C with 600-1150 mm of precipitation, mainly as rain in the summer. Mixed coniferous forests are found on spodosols, alfisols, and inceptisols.

Nitrogen: 40% of the streams with low and 40% with medium concentrations

Phosphorus: 38% of the streams have low concentrations and 47% have high

Sediment: Low in all streams

Land Use: Approximately 70% forest

Hardness: Soft, medium, and hard; 50% of the streams soft and 30% hard

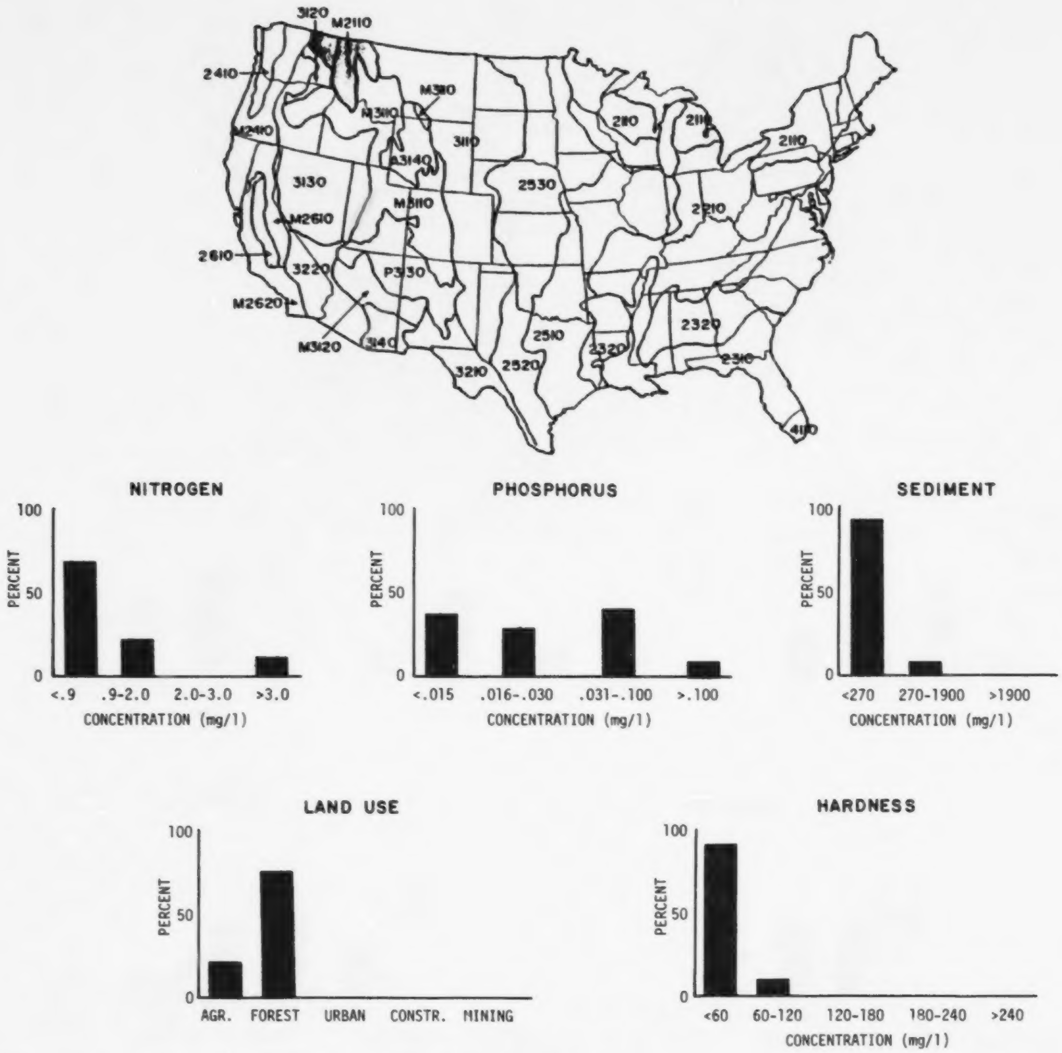


Fig. 5.5. Province M2110 - COLUMBIA FOREST

The Columbia Forest is a province of 45,300 mi^2 found in northeastern Washington, northern Idaho, and northwestern Montana. Precipitation of 500-1000 mm (average annual) is distributed in the fall, winter, and spring. The province has mixed coniferous-deciduous forests over inceptisols.

Nitrogen:	Low concentrations (70% of the streams), medium and very high (8% of the streams)
Phosphorus:	Approximately 35% of the streams with low and 40% with high concentrations
Sediment:	Generally low - 95% of the rivers
Land Use:	Approximately 75% forest and 23% agriculture
Hardness:	Soft water (95%)

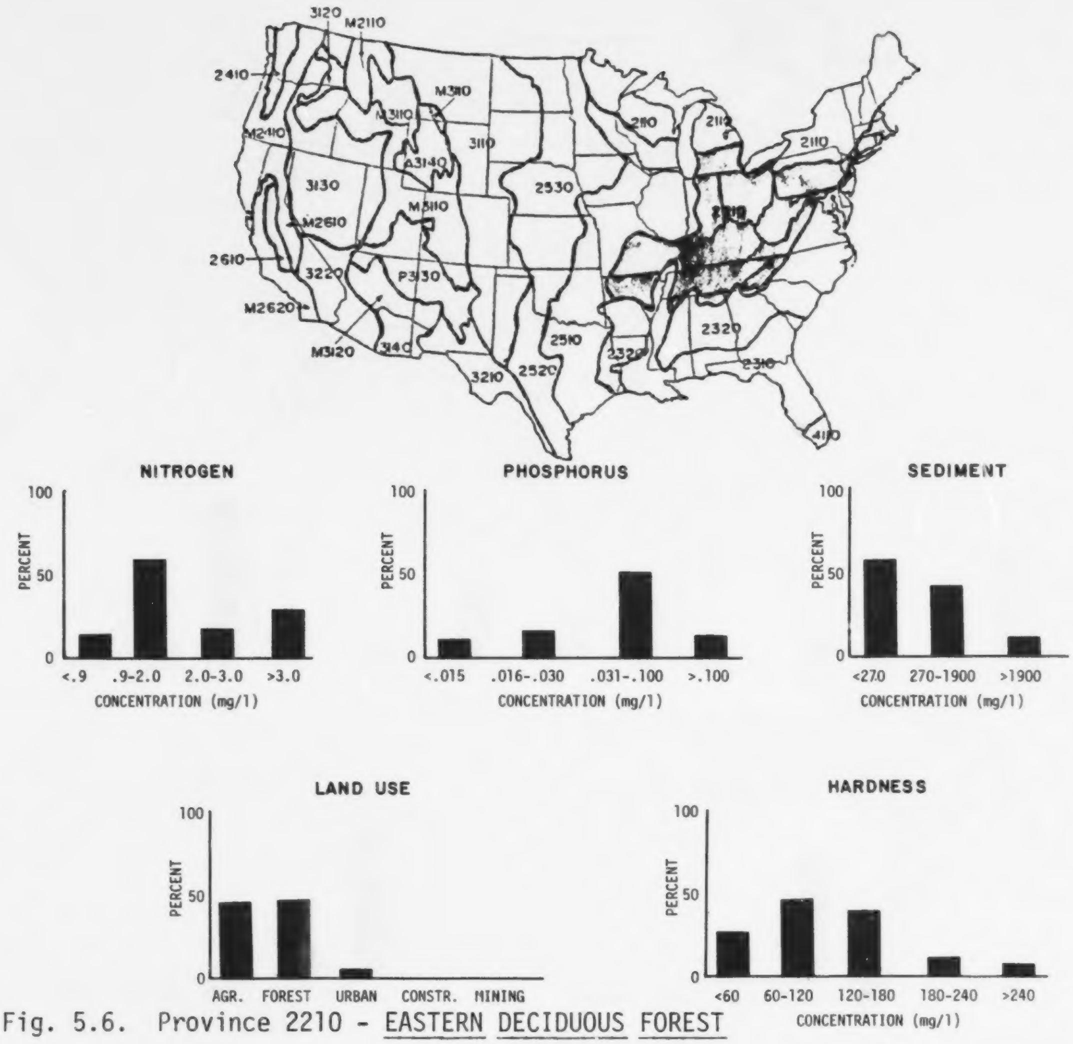


Fig. 5.6. Province 2210 - EASTERN DECIDUOUS FOREST

The large Eastern Deciduous Forest Province of 367,800 mi^2 encompasses most of eastern United States, namely southern New England, Pennsylvania, western Virginia, Maryland, and North Carolina, Tennessee, Kentucky, West Virginia, Ohio, eastern Indiana, southern Illinois, southern Missouri, and northern Arkansas. The average annual temperatures are 4-15° C. The average annual percipitation, which falls mainly in the summer, is 900-1500 mm. The soils are primarily inceptisols and ultisols and the area is dominated by temperate deciduous forest.

Nitrogen: Medium concentrations (63% of the streams), high, and very high concentrations

Phosphorus: Generally high--approximately 63% of the streams

Sediment: Primarily low (60% of streams) to medium (35%) concentrations

Land Use: Approximately 49% agriculture and 49% forest

Hardness: Soft to hard--40% of streams medium, 40% hard

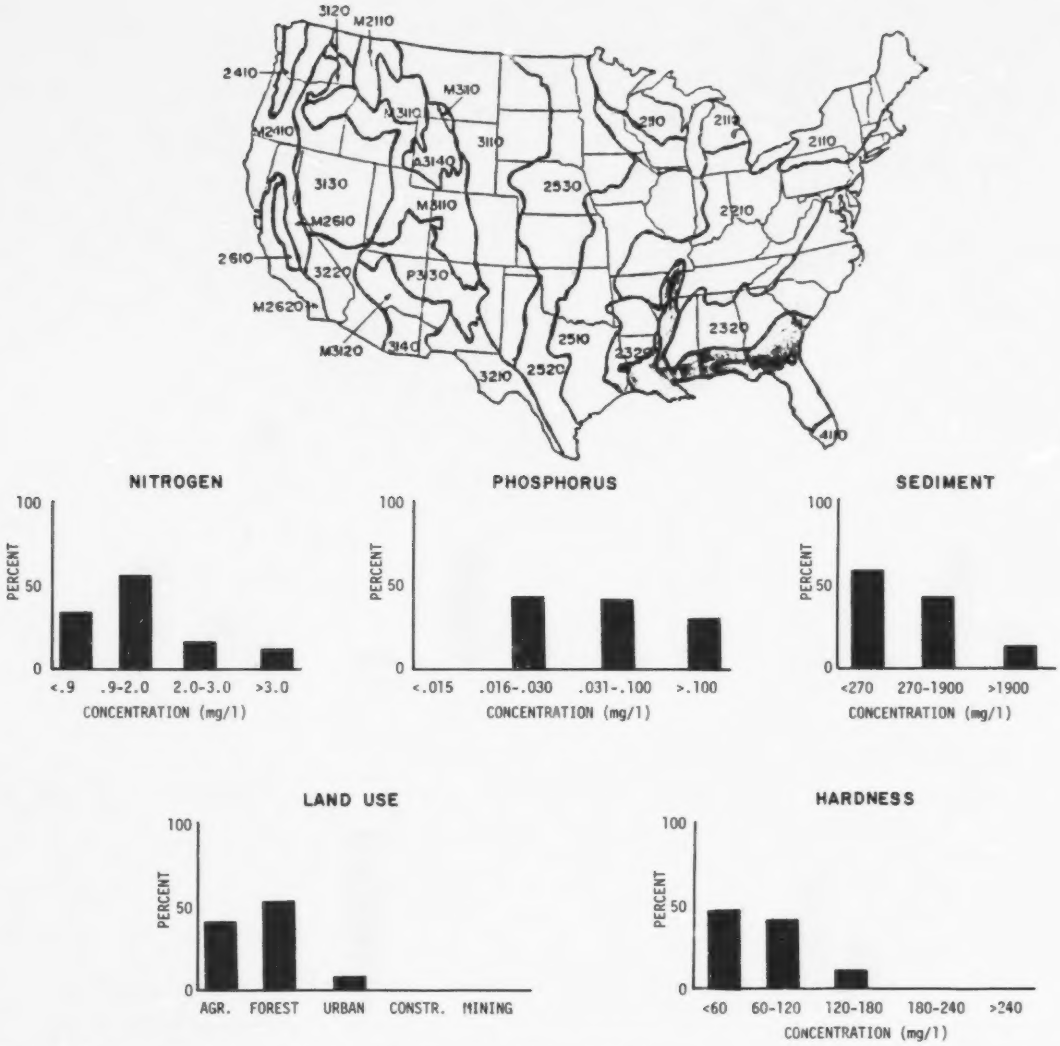


Fig. 5.7. Province 2310 - OUTER COASTAL PLAIN

The Outer Coastal Plain (150,100 mi^2) is the area of southern Georgia, Alabama, and Mississippi, the southern Mississippi River Basin from southern Illinois to southern Louisiana, and north and central Florida. The average annual temperature is 15-21° C. Precipitation, common throughout the year, is 1000-1525 mm (average annual). Temperate evergreen forests are found on entisols, alfisols, and ultisols.

Nitrogen: Generally medium concentrations (58% of streams) with low and high equal

Phosphorus: Medium (45% of streams) to high concentrations

Sediment: Low (approximately 66% of the streams) to medium concentrations

Land Use: Approximately 40% agriculture and 58% forest

Hardness: Generally soft to medium-hard water

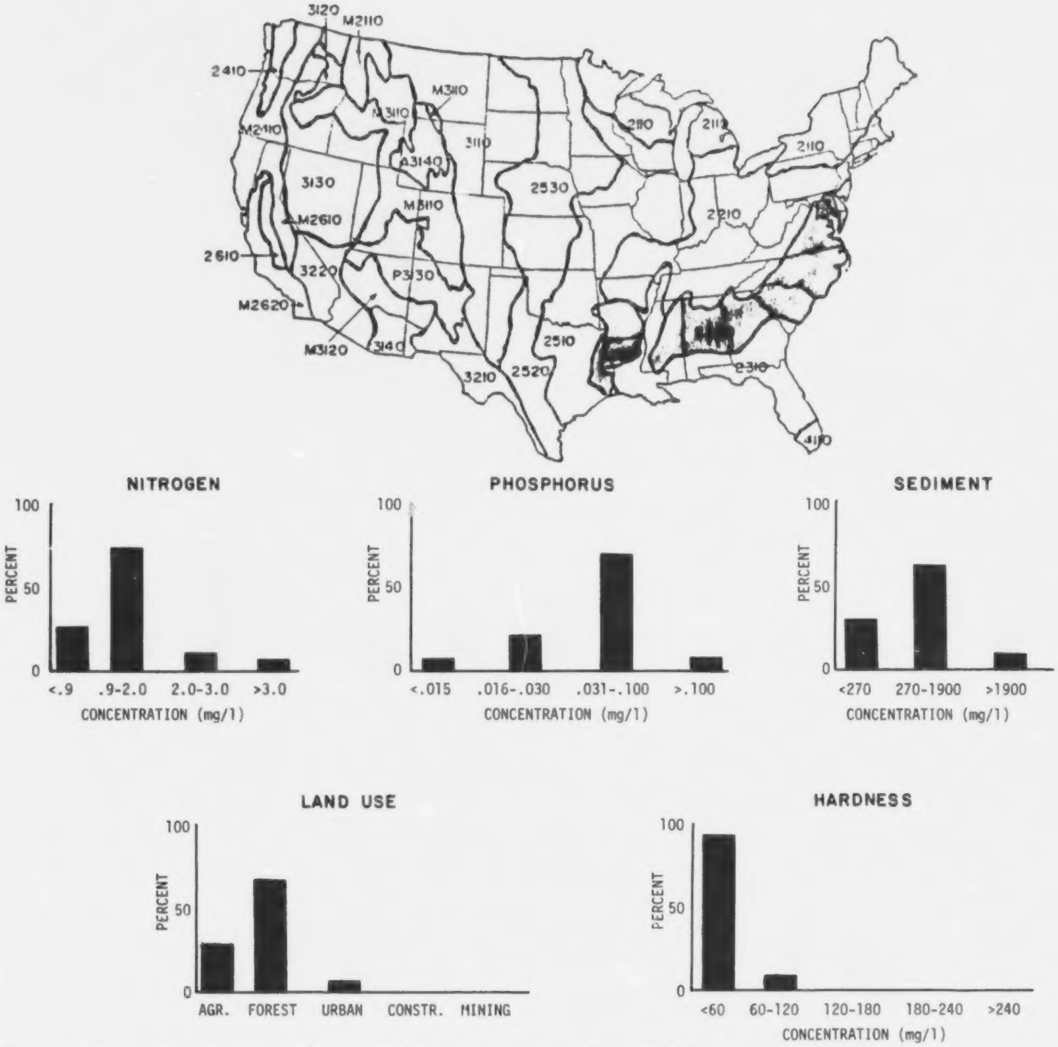


Fig. 5.8. Province 2320 - SOUTHEASTERN MIXED FOREST

The Southeastern Mixed Forest comprises 257,900 mi^2 of coastal Virginia, North Carolina, and South Carolina, central and northern Georgia and Alabama, eastern Mississippi, northwest Louisiana, southwest Arkansas, small section of southeast Oklahoma and eastern Texas. Temperatures average 15-21^o per year and precipitation averages 1000-1500 mm per year with a slight summer peak. Ultisols and inceptisols support a mixed deciduous-evergreen forest.

Nitrogen: Medium concentrations in 75% of the streams

Phosphorus: High concentrations in approximately 80% of the streams

Sediment: Low and medium (65% of the streams) concentrations

Land Use: 66% forest

Hardness: Soft water

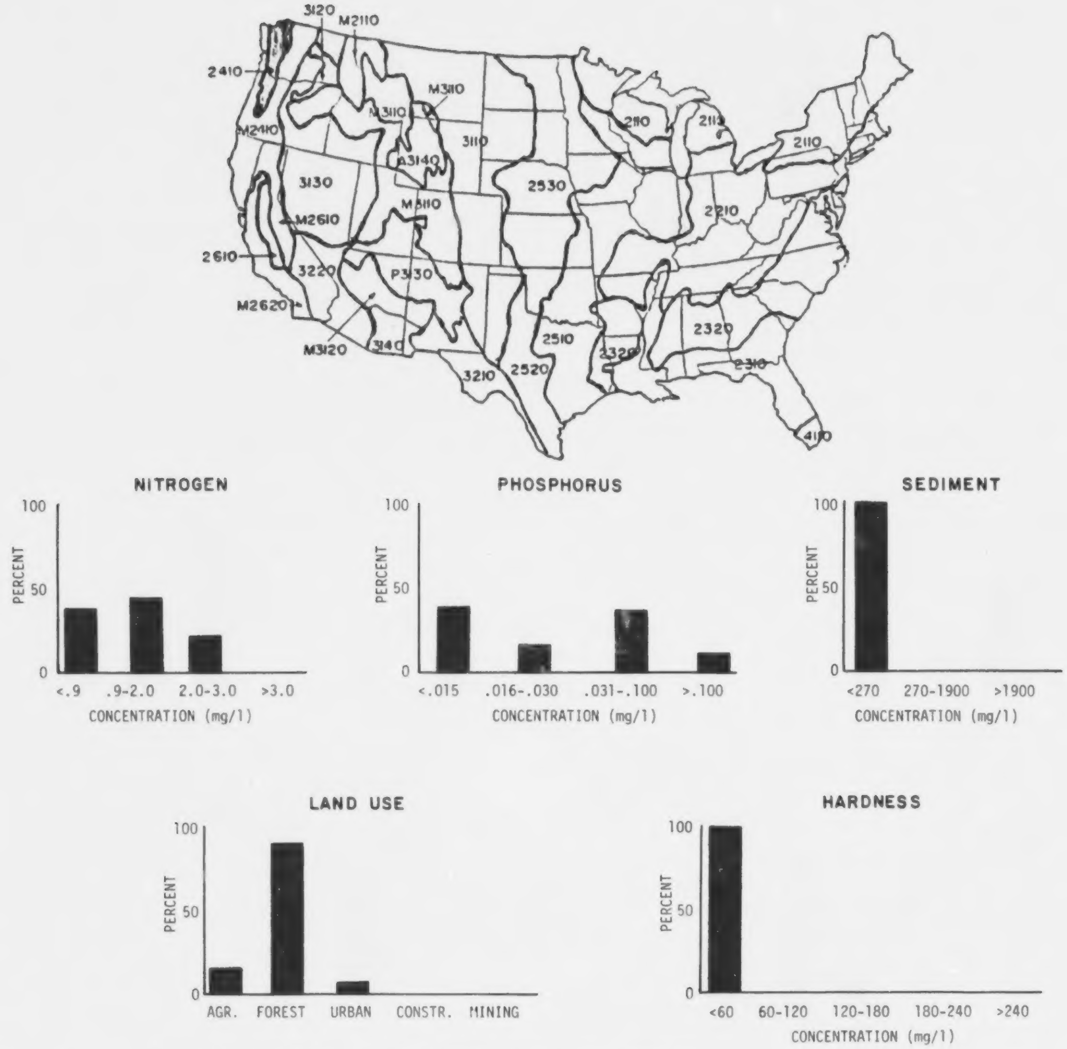


Fig. 5.9. Province 2410 - WILLAMETTE-PUGET FOREST

The small Willamette-Puget Forest province, 13,000 mi^2, includes the coniferous forests of west central Washington and north central Oregon. The average annual temperature is 9-13° C, with precipitation greatest in the summer with 380-1525 mm average per year. The soils are alfisols, inceptisols, and ultisols.

Nitrogen: Concentrations are predominantly low (37% of the streams) and medium (47%)

Phosphorus: Low (40% of streams) to high (45%) concentrations

Sediment: All streams with low concentrations

Land Use: 85% forest

Hardness: All soft water

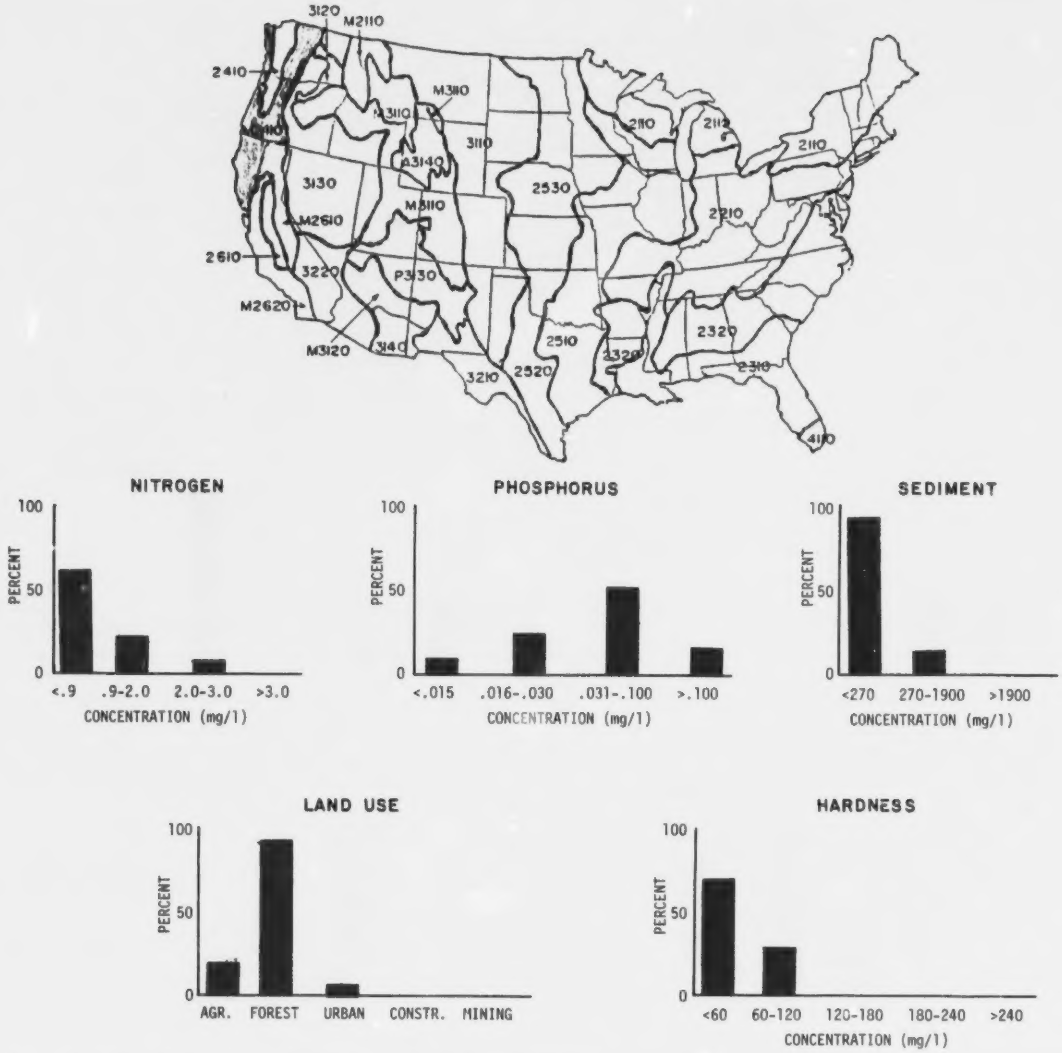


Fig. 5.10. Province M2410 - PACIFIC FOREST

The Pacific Forest occupies coastal and central Washington and Oregon, and northwestern California, an area of 129,700 mi^2. Average annual temperatures are 2-10° C. Precipitation occurs predominantly in the winter averaging 750-3800 mm per year. Coniferous forests predominate and ultisols and inceptisols are common.

Nitrogen: Low (68% of the streams) and medium concentrations

Phosphorus: Mainly medium and high (67% of the streams) concentrations

Sediment: 80% of the streams with low concentrations; 20% medium

Land Use: 75% forest

Hardness: Water is soft (about 75% of the streams) to medium hard

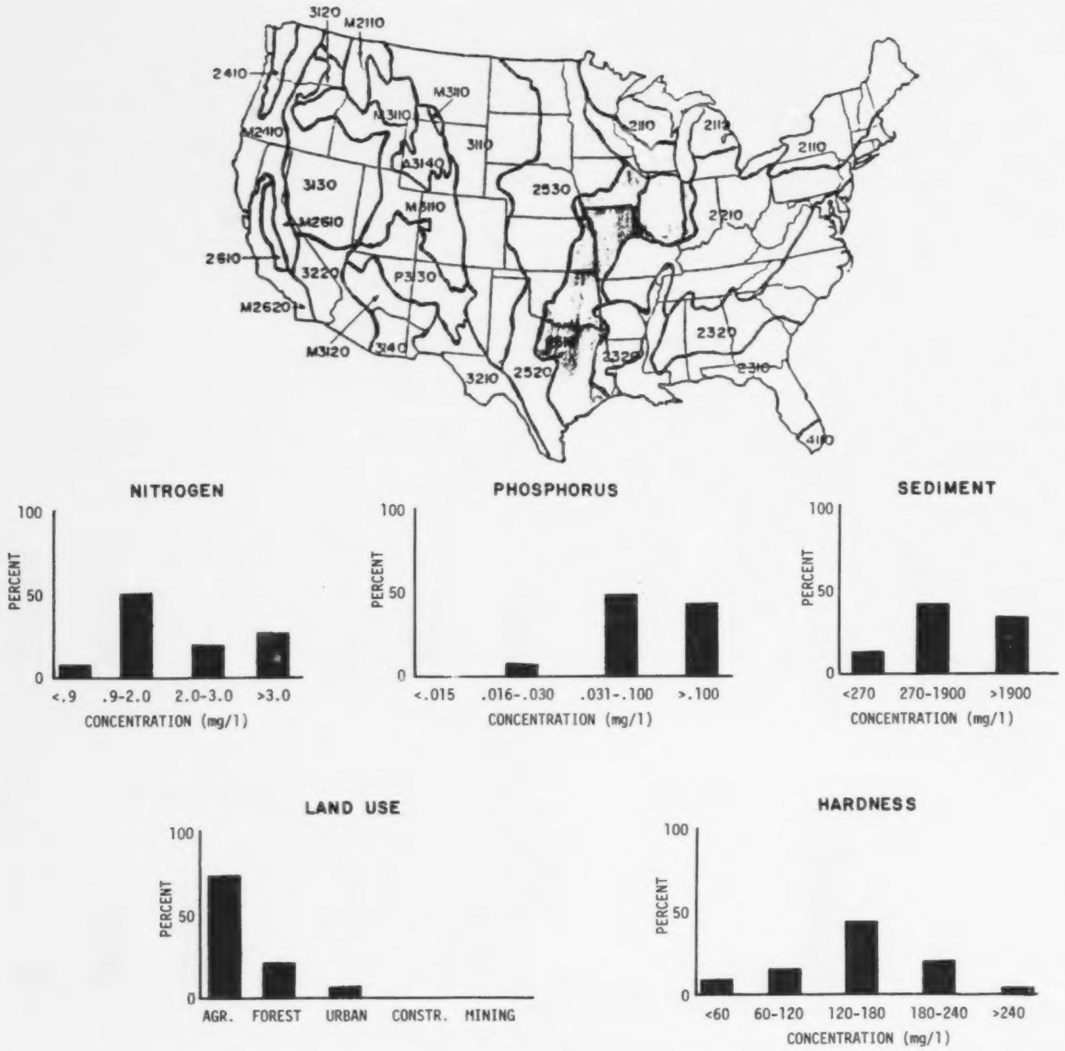


Fig. 5.11. Province 2510 - PRAIRIE PARKLAND

The large Prairie Parkland province, 204,600 mi^2, encompasses Illinois, southern Iowa, northern Missouri, southeastern Kansas, eastern Oklahoma, and a portion of east Texas. The area has a mean annual temperature of 13-21° C and 600-1000 mm of precipitation with a maximum in the summer. Mollisols, alfisols, and vertisols support a forest steppe and prairie deciduous vegetation.

Nitrogen: Medium (52% of streams) and high concentrations

Phosphorus: 95% of the streams with high concentrations

Sediment: Medium (52% of streams) and high (40%) concentrations

Land Use: About 78% agricultural

Hardness: Hard water

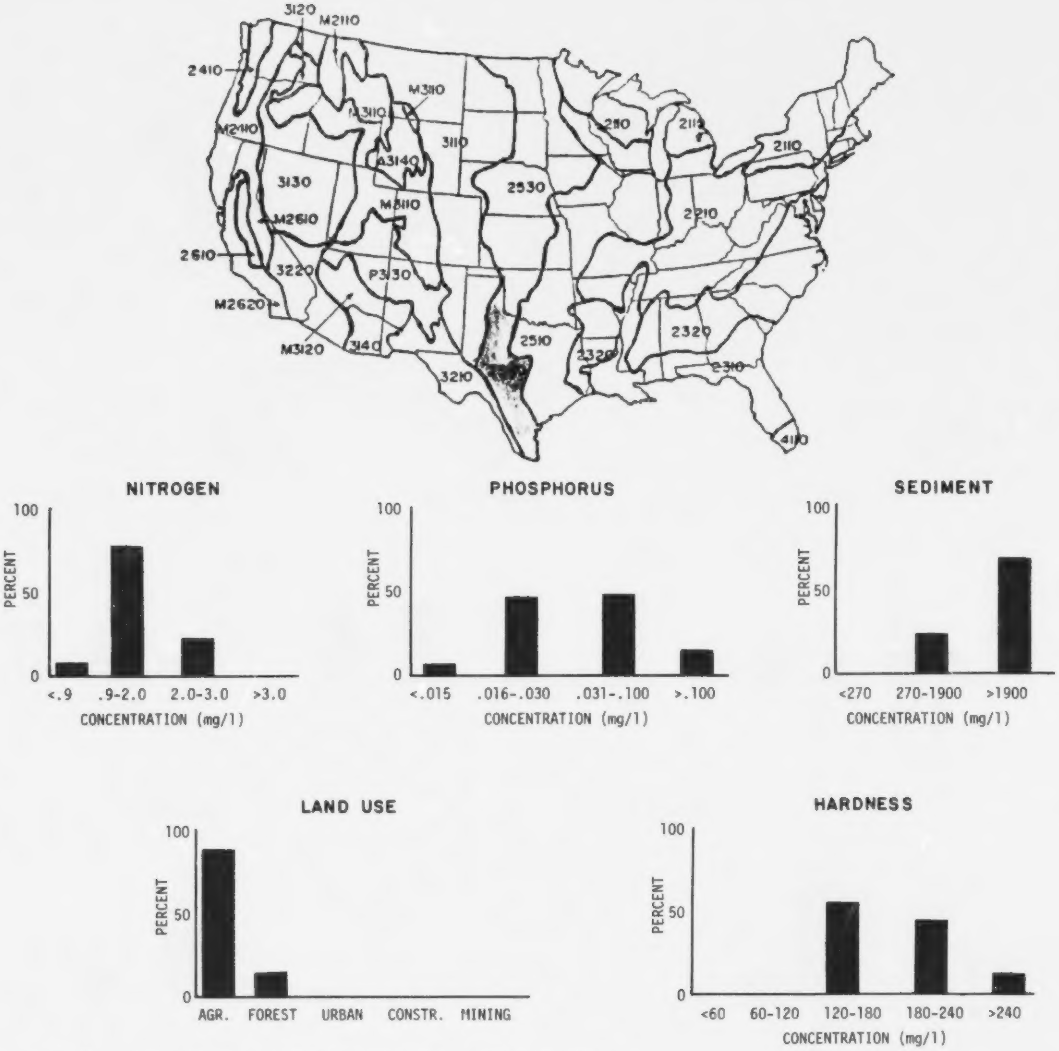


Fig. 5.12. Province 2520 - PRAIRIE BRUSHLAND

The Prairie Brushland Province, an area of 83,600 mi^2, is found in central Texas. This province has 15-21° C average annual temperatures. Precipitation occurs mainly in the summer with a mean annual input of 500-750 mm, but annual evaporation is 1800-200 mm.. Mollisols, entisols, and alfisols and arid grasslands characterize the province.

Nitrogen: Medium (68% of streams) to high concentrations

Phosphorus: 42% of streams medium, and 55% high concentrations

Sediment: High concentrations, approximately 65% of streams

Land Use: 86% agriculture, primarily rangeland

Hardness: Waters are hard

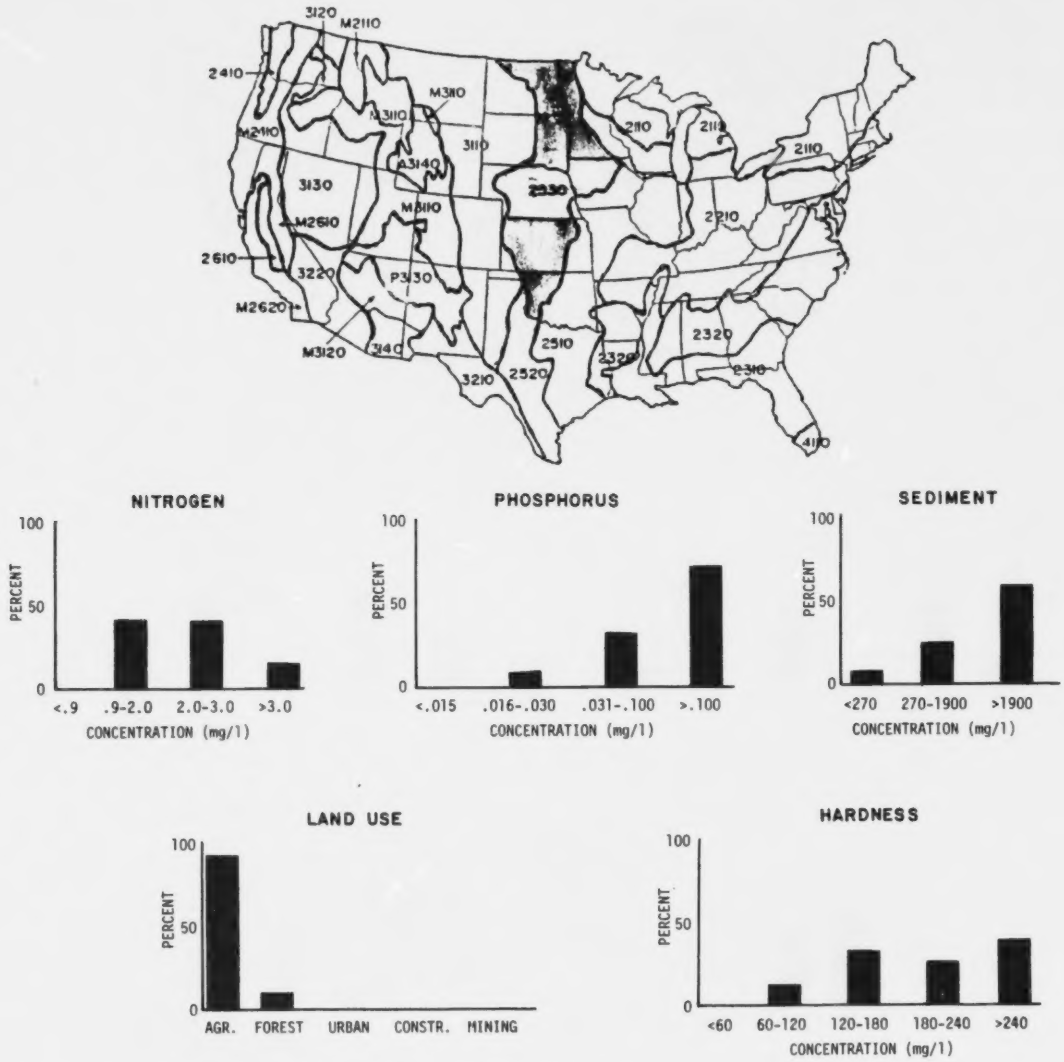


Fig. 5.13. Province 2530 - TALL GRASS PRAIRIE

The Tall Grass Prairie Province encompasses 223,000 mi^2 of eastern portions of North and South Dakota, western Minnesota, northwest Iowa, Nebraska, Kansas, and central Oklahoma. Temperature and precipitation vary throughout the region with mean annual temperatures of 4-18° C and mean annual precipitation of 380-600 mm. Mollisols support intensive agriculture.

Nitrogen: Medium and high concentrations (42% of streams each)

Phosphorus: Very high concentration--approximately 66% of streams

Sediment: High concentrations--approximately 65% of streams

Land Use: 95% agriculture

Hardness: Water is hard

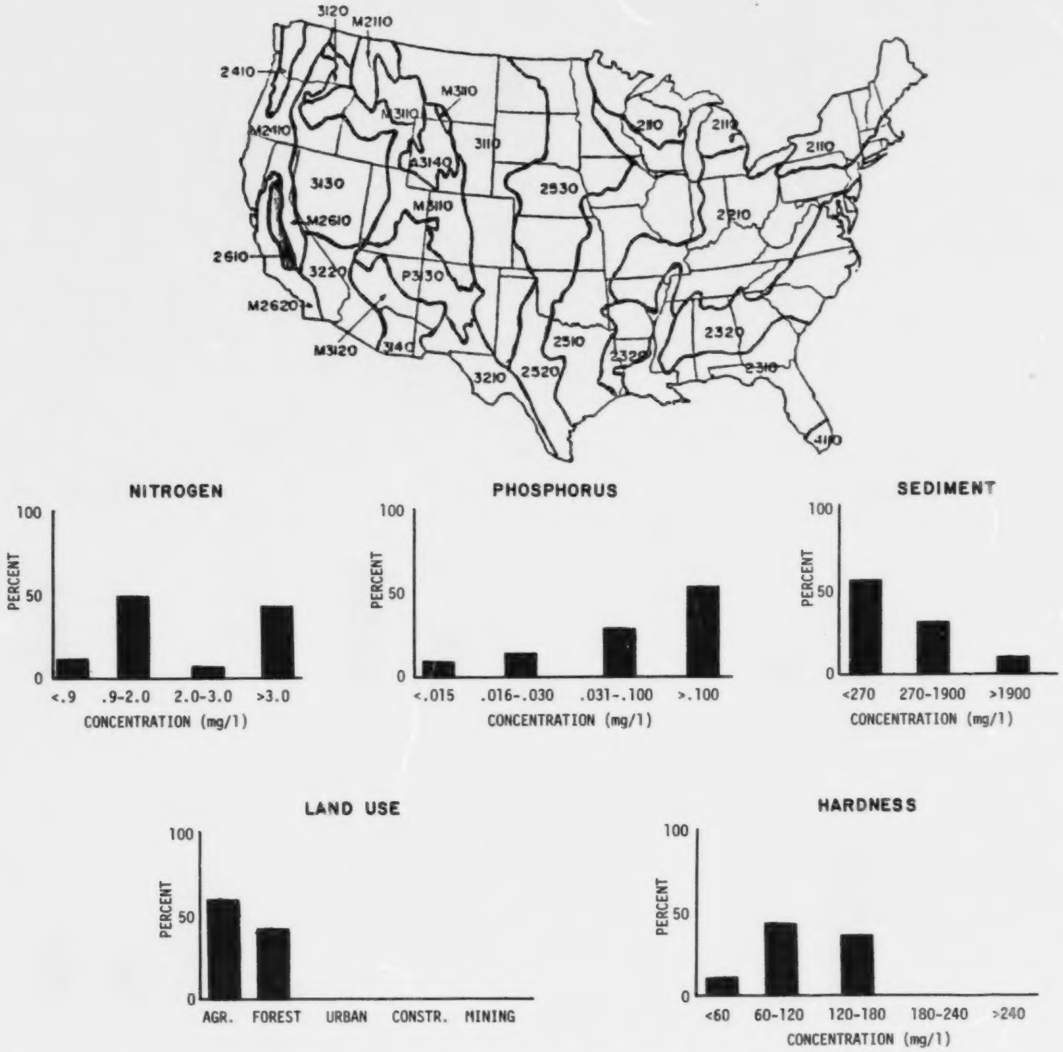


Fig. 5.14. Province 2610 - CALIFORNIA GRASSLAND

The California Grassland is restricted to the central valley of California, an area of 20,200 mi^2. It has average annual temperatures of 15-19^{o} C and low precipitation of 150-160 mm annual, falling primarily in winter. This region of intensive agriculture has introduced annual grass and mollisols.

Nitrogen: 42% of streams have medium and 51% very high concentrations

Phosphorus: Generally high; 57% of streams with very high concentrations

Sediment: Generally low concentration--60% of streams, and medium (35%)

Land Use: Approximately 60% agriculture

Hardness: Medium to hard water

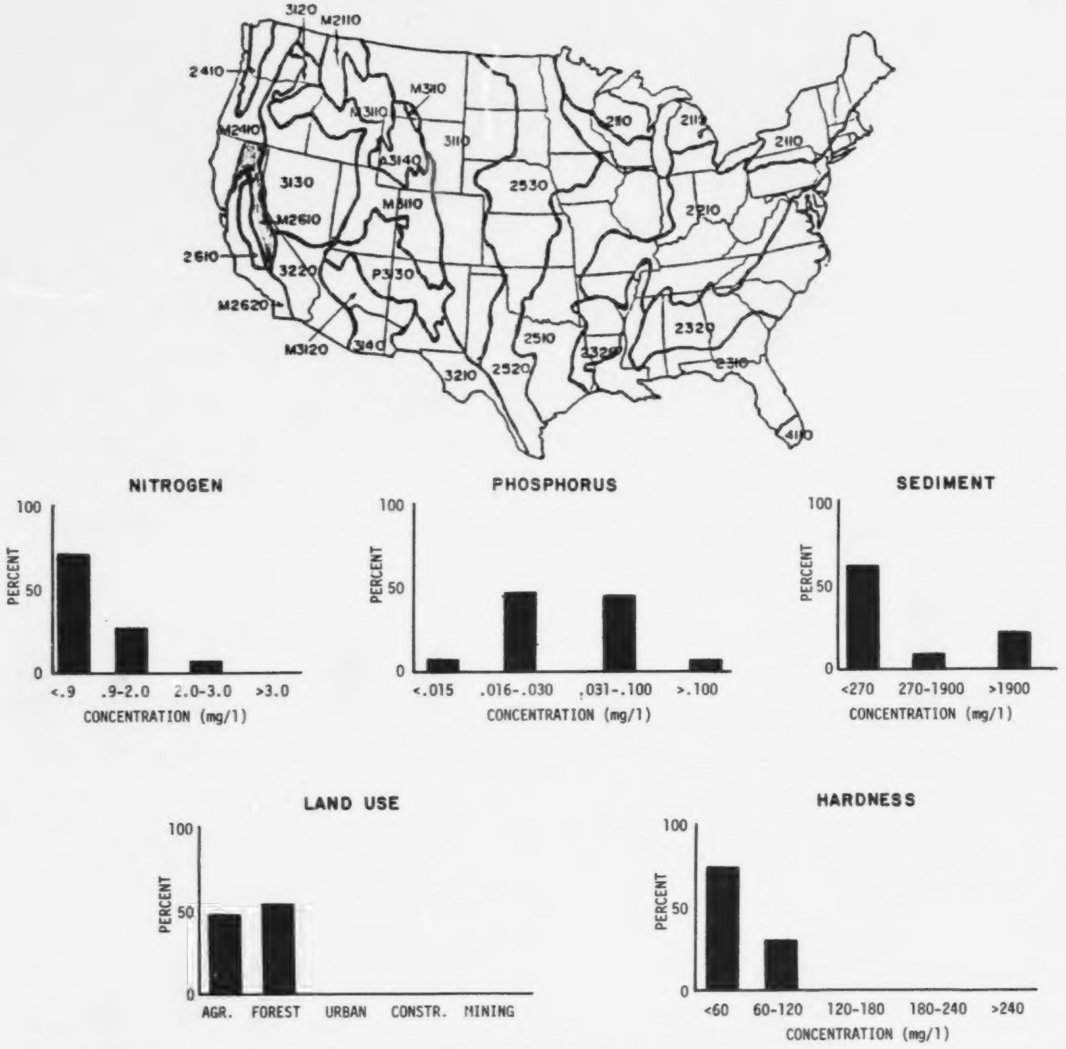


Fig. 5.15. Province M2610 - SIERRAN FOREST

The Sierran Forest encompasses most of eastern California in the Sierra Nevada mountains. Temperatures average 2-11° C yearly. Precipitation in the province is 250-1800 mm with a summer dry period and a winter maximum. The soils are vertisols, alfisols, and entisols and the vegetation is chaparral to mixed conifer forest depending upon altitude.

Nitrogen: 70% of the streams have low and 28% have medium concentrations

Phosphorus: Medium (48% of the streams) to high (42%) concentrations

Sediment: Generally low--64% of the streams; 17% with high concentrations

Land Use: 55% forest and 45% agriculture

Hardness: 75% of the water is soft; remainder medium-hard

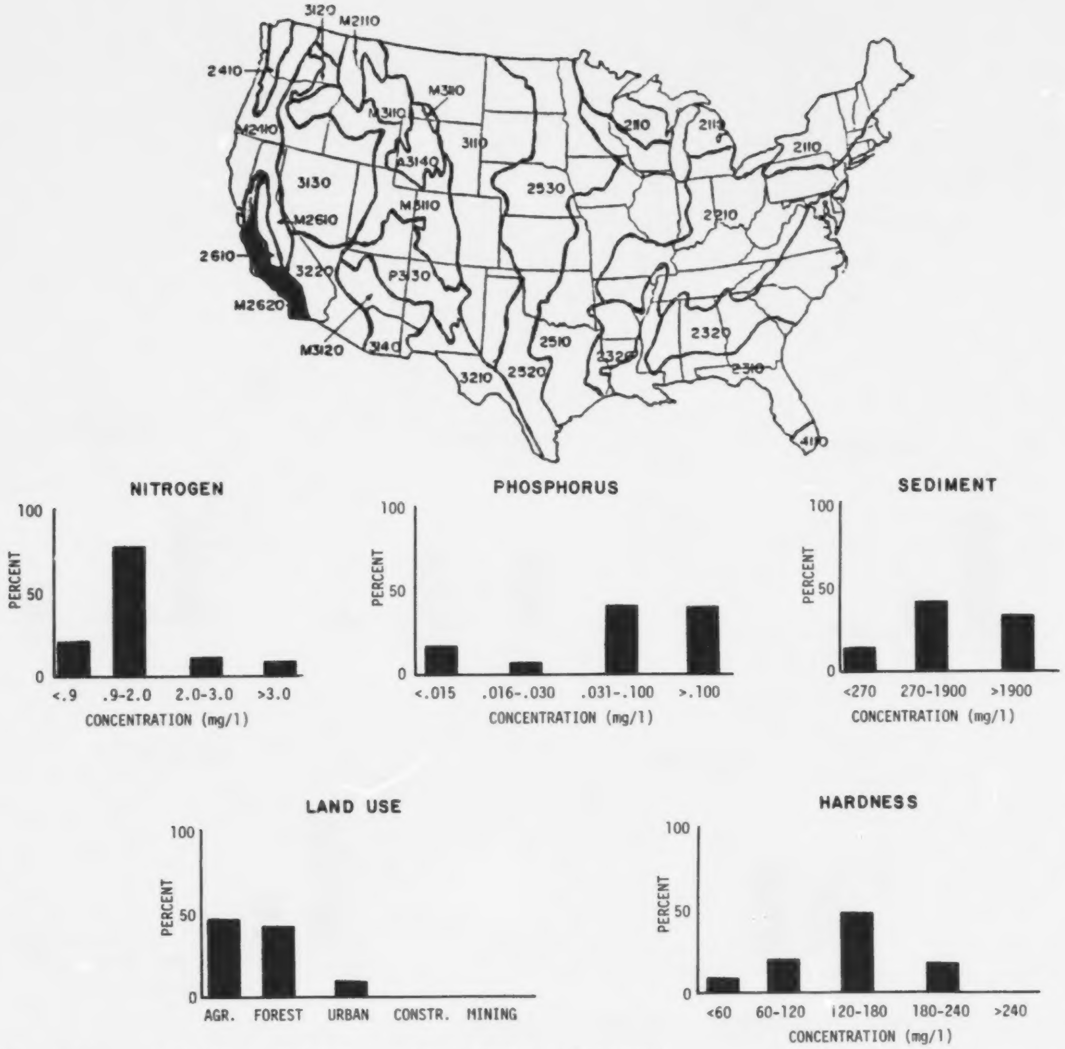


Fig. 5.16. Province M2620 - CALIFORNIA CHAPARRAL

The California Chaparral Province comprises 33,500 mi^2 of southwestern California. This is a dry area of 300-1000 mm of precipitation yearly, with a summer dry period and yearly temperatures averaging 13-18° C. Chaparral and sclerophyll forest dominate on mollisols, alfisols, and entisols.

Nitrogen: 71% of the streams have medium concentrations

Phosphorus: 85% of the streams with high concentrations

Sediment: 41% of the streams with medium concentrations and 40% with high

Land Use: 51% agriculture, 4% urban

Hardness: Generally hard water

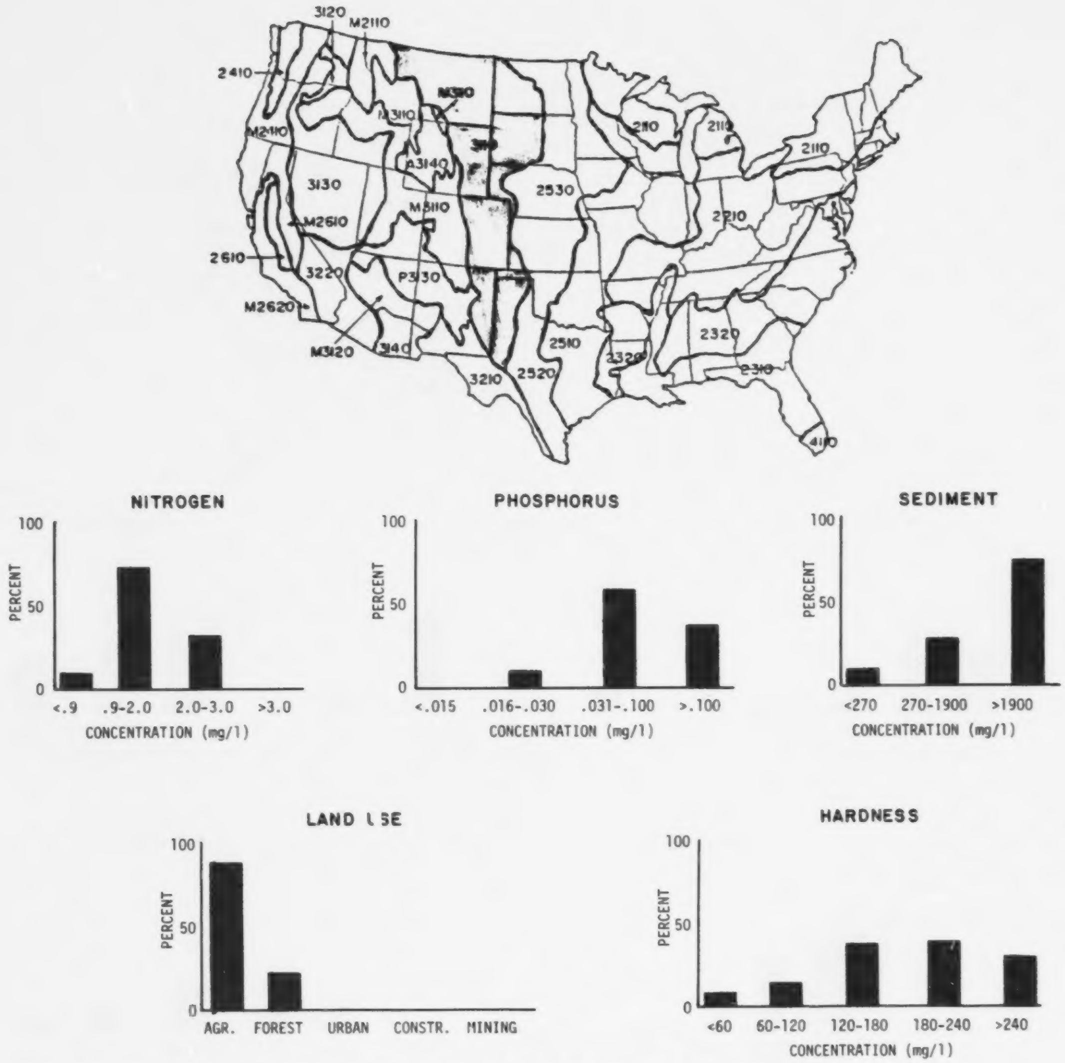


Fig. 5.17. Province 3110 - GREAT PLAINS SHORT GRASS PRAIRIE

The Great Plains Short Grass Prairie province is a large (317,500 mi^2) region of the western Dakotas, a small portion of western Nebraska, western Kansas, Oklahoma and Texas panhandles, and the eastern portion of Montana, Wyoming, Colorado, and New Mexico. Temperatures range from 8-15° C (average annual) and precipitation is 259-620 mm annually with maximum input in the summer. Evaporation is greater than precipitation. The dominant natural vegetation in this heavily agricultural area is shortgrass prairie and the soils are generally mollisols.

Nitrogen: 70% of the streams medium and 24% high concentrations

Phosphorus: 98% of streams with high concentrations

Sediment: 74% of the streams high concentrations and 25% medium

Land Use: 90% agricultural

Hardness: Predominantly hard water

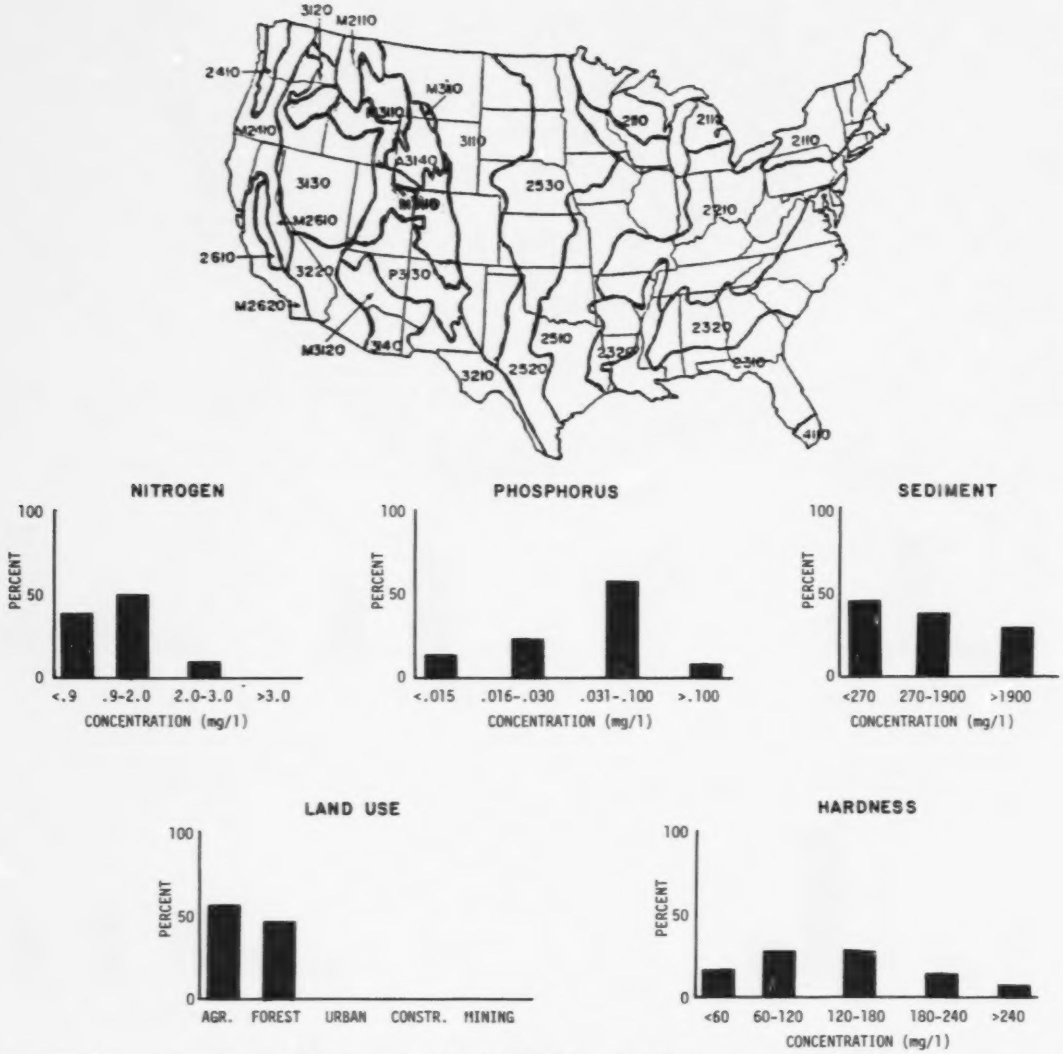


Fig. 5.18. Province M3110 - ROCKY MOUNTAIN FOREST

The Rocky Mountain Forest is found in eastern Oregon, central Idaho, southwestern Montana, western Wyoming, eastern Utah, western Colorado, and north central New Mexico, covering 187,300 mi^2. Average annual temperatures are low, 2-10^{o} C, and precipitation 250-1000 mm annually with a winter maximum in the form of snow. Mollisols and alfisols to aridisols are the dominant soils and alpine and mixed coniferous forest are the dominant vegetation.

Nitrogen: 41% of streams have low and 52% have medium concentrations

Phosphorus: High concentrations (65% of streams); low concentrations (22%)

Sediment: Low, medium, and high concentrations; 45% of the streams have low concentrations

Land Use: 52% agriculture, predominantly range

Hardness: Soft, medium-hard, and predominantly hard (46% of streams)

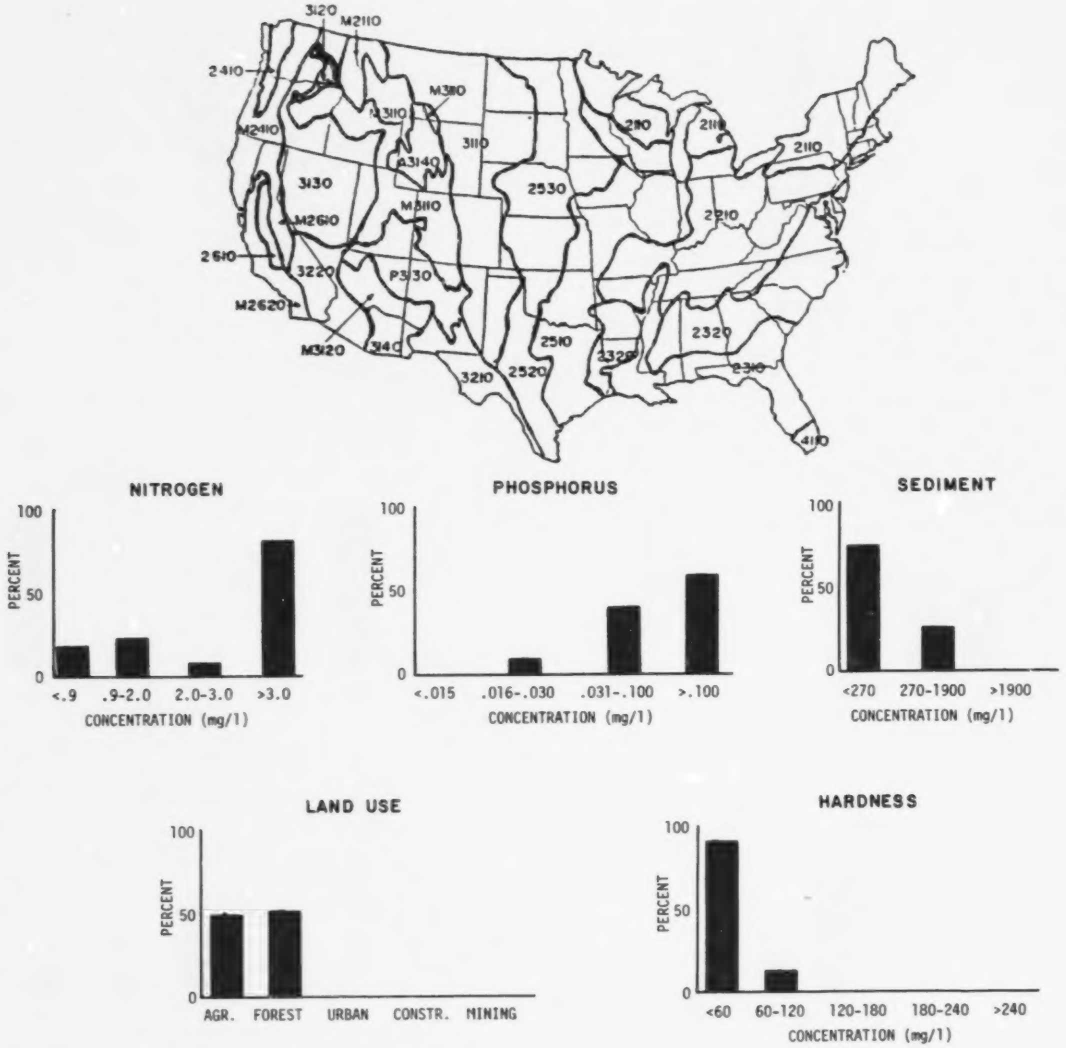


Fig. 5.19. Province 3120 - PALOUSE GRASSLAND

The small (12,400 mi^2) Palouse Grassland province is found in southeastern Washington and northeastern Oregon. Average temperatures range from 7-13° C annually and precipitation is 450-600 mm per year--primarily in the winter. Natural vegetation is sagebrush and prairie grasses on mollisols.

Nitrogen: 68% of the streams have very high and 21% have medium concentrations

Phosphorus: 93% of streams have high concentrations

Sediment: 75% of the streams with low concentrations

Land Use: Approximately 50% agriculture and 50% forest

Hardness: Soft water

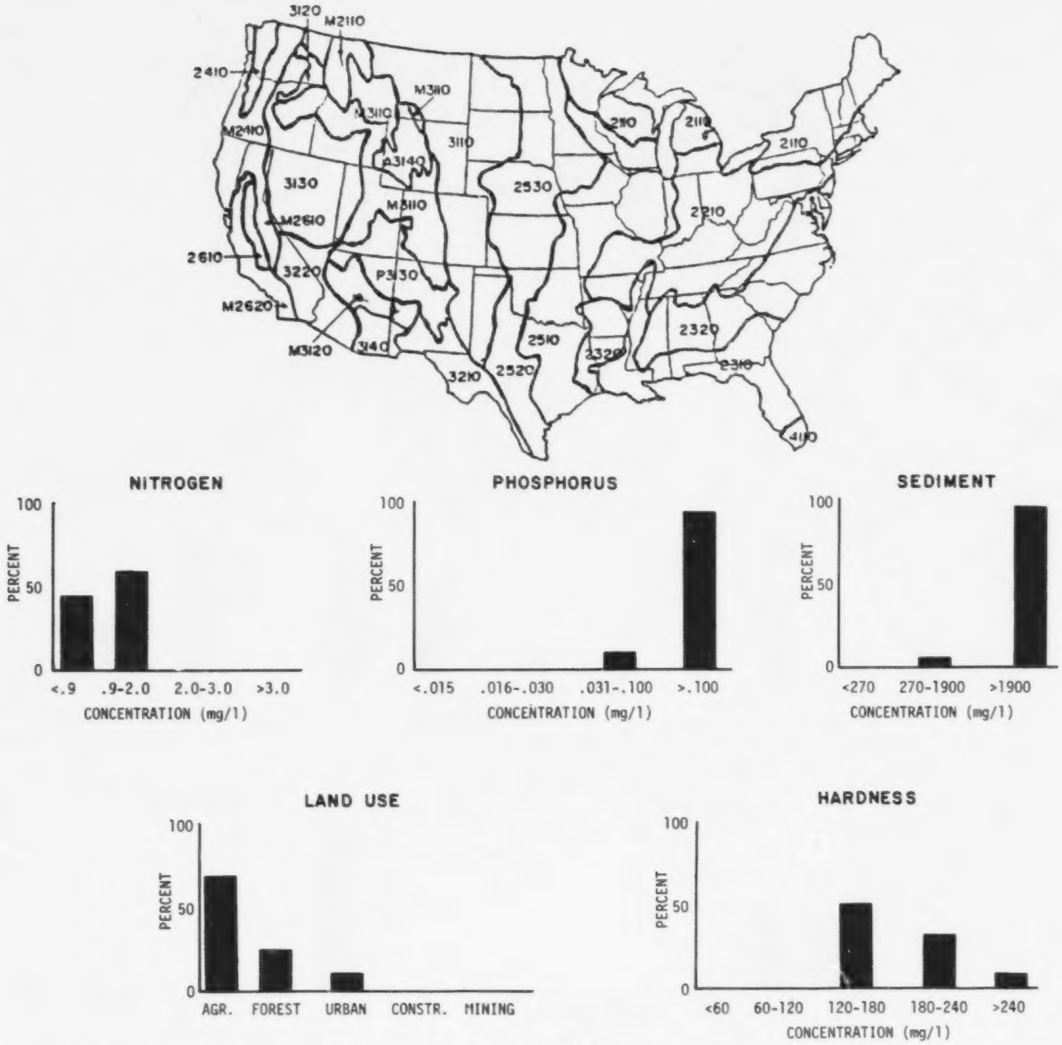


Fig. 5.20. Province M3120 - UPPER GILA MOUNTAIN FOREST

The Upper Gila Mountain Forest province, found in central Arizona and west central New Mexico, is 31,100 mi^2. Average annual temperatures are 5-13° C. Precipitation is variable with early autumn, winter, and summer thunderstorms, and input averages 250-875 mm annually. Grasses and chaparral are found at low elevations and mixed coniferous forest dominates the mountains. The soils are mollisols, aridisols, and entisols.

Nitrogen: Low and medium concentrations; 64% of streams with medium

Phosphorus: 94% of streams with high concentrations

Sediment: 98% of streams with high concentrations

Land Use: 70% agriculture primarily range

Hardness: Hard water

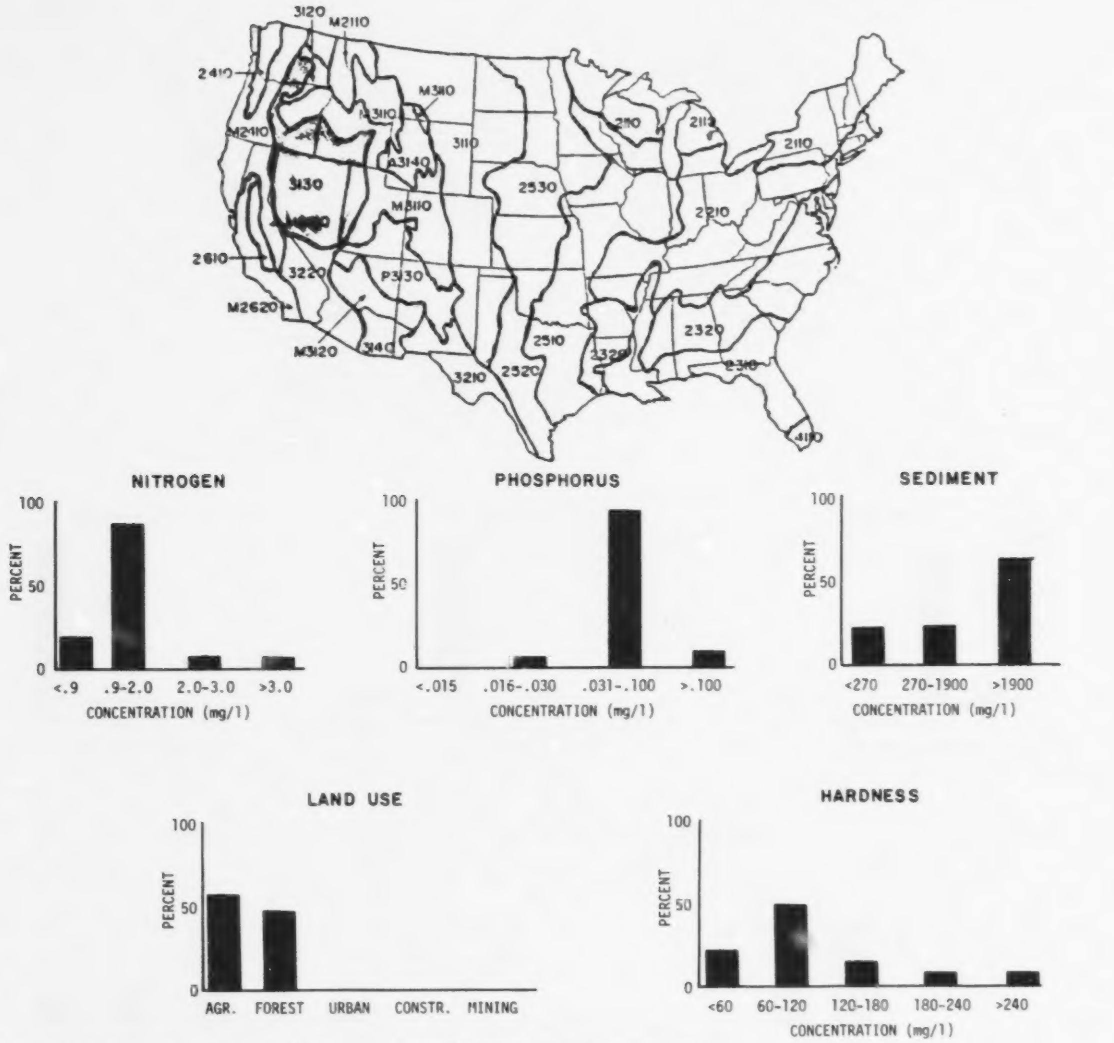


Fig. 5.21. Province 3130 - INTERMOUNTAIN SAGEBRUSH

The Intermountain Sagebrush Province (203,400 mi^2) is essentially the Great Basin of southeastern Oregon, southern Idaho, western Utah, most of Nevada, and portions of northeastern California. This dry region has average annual temperatures of 4-18° C with precipitation of 125-500 mm yearly. Precipitation is highest in the winter with none in the lowlands during the summer. The area is dominated by sagebrush and has mixed coniferous forest at higher elevations. The soils are aridisols and mollisols.

Nitrogen: 78% of streams have medium concentrations

Phosphorus: 97% of the streams have high concentrations

Sediment: Low, medium, and high; 43% of the streams have high concentrations

Land Use: 60% agriculture, primarily range

Hardness: Soft, medium hard, and hard; 50% of streams medium hard

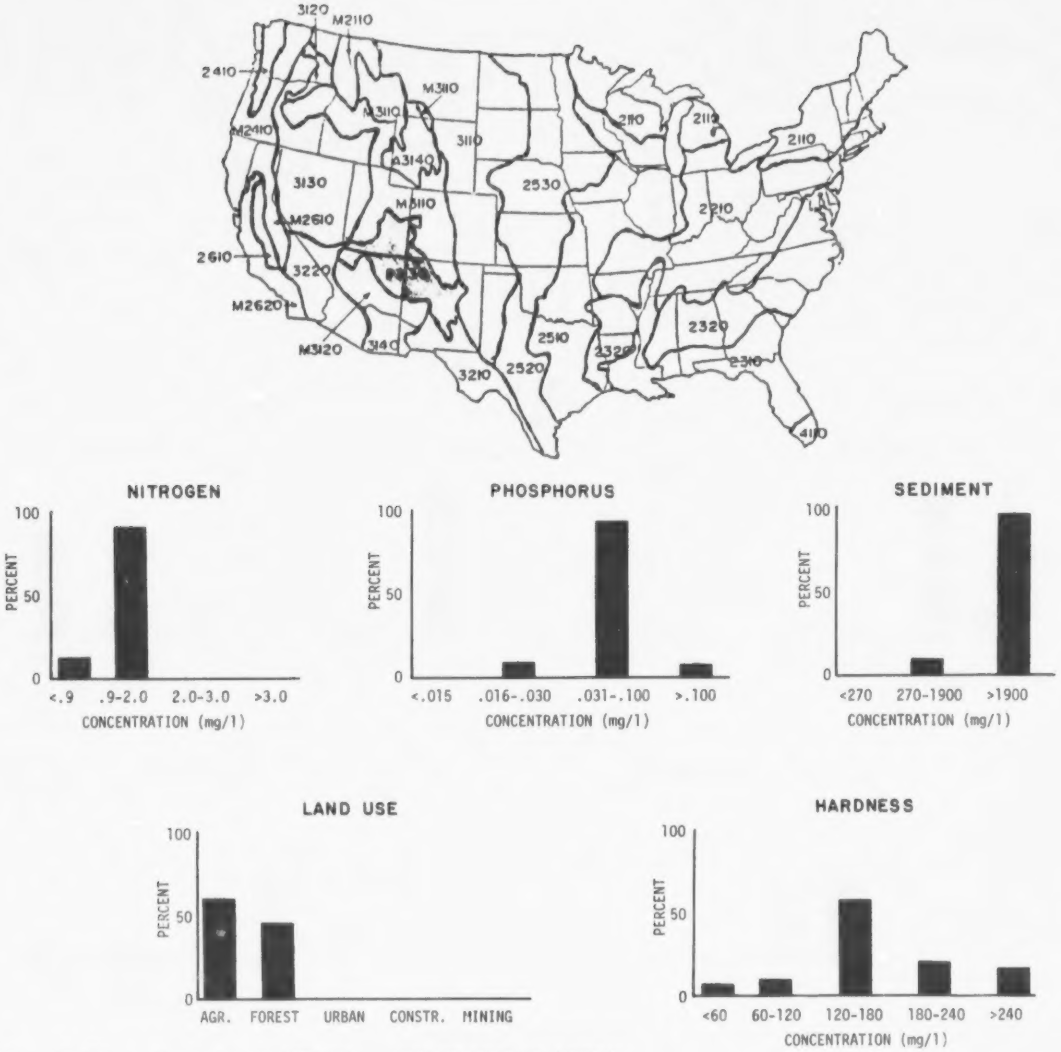


Fig. 5.22. Province P3130 - COLORADO PLATEAU

The Colorado Plateau of southeastern Utah, northern Arizona, southwestern Colorado, northwest and central New Mexico is an area of 94,700 mi^2. This is a dry region of less than 500 mm of precipitation yearly which results from winter and summer thunderstorms. Entisols and aridisols support arid grassland, pinyon pine, and coniferous forest.

Nitrogen: 93% of streams have medium concentrations

Phosphorus: 96% of streams have high concentrations

Sediment: 96% of streams have high concentrations

Land Use: 53% agriculture

Hardness: Hard water

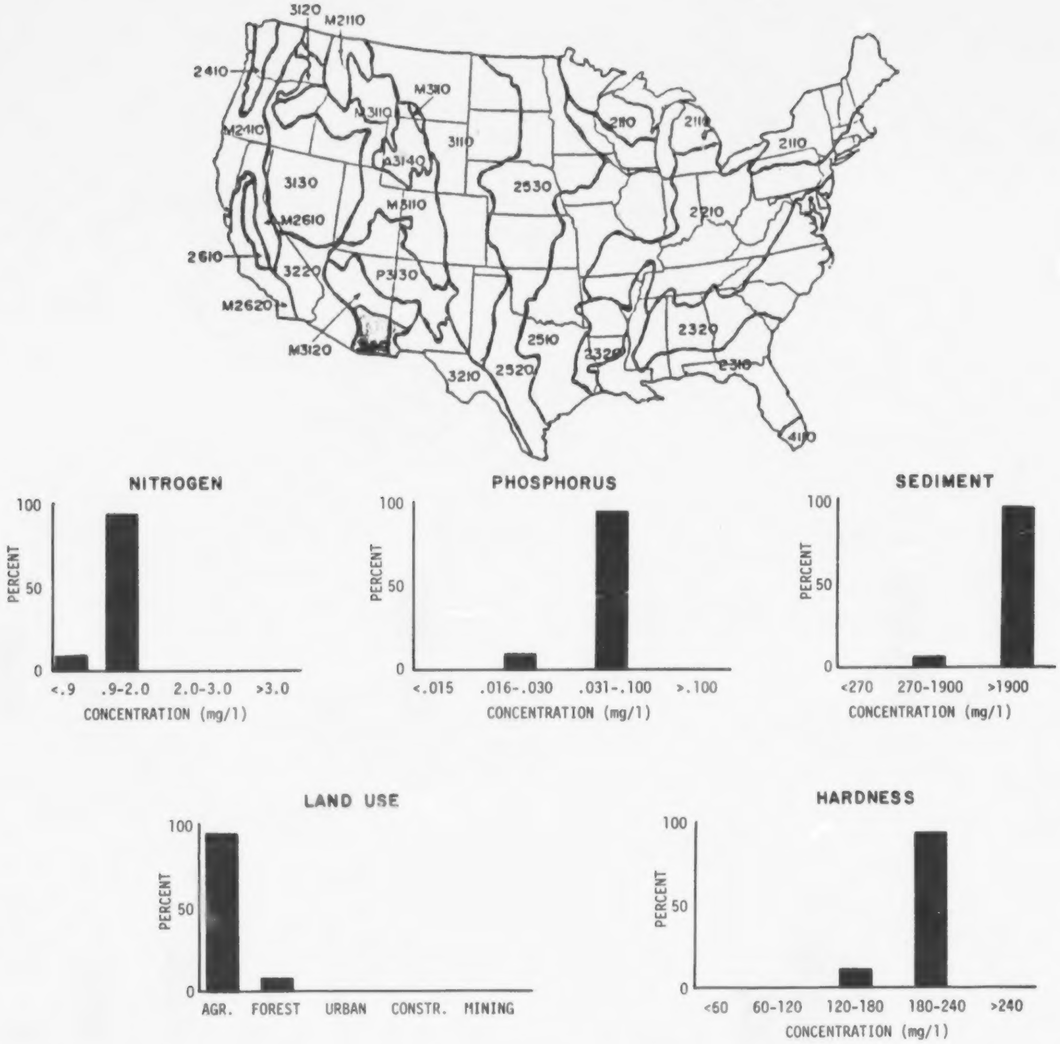


Fig. 5.23. Province 3140 - MEXICAN HIGHLANDS SHRUB STEPPE

The Mexican Highlands Shrub Steppe province of southwest New Mexico and southeast Arizona is an area of 17,500 mi^2. Temperatures of 13-21° C (average annual) and very low precipitation from summer thunderstorms and occassionally some input in winter, characterize the area. Aridisols support cactus, creosote bush, and short grasses in the lowlands and oaks, junipers, and conifers at higher elevations.

Nitrogen: 97% of the streams have medium concentrations

Phosphorus: 95% of the streams have high concentrations

Sediment: 92% of the streams have high concentrations

Land Use: 80% agriculture (range)

Hardness: All water is hard

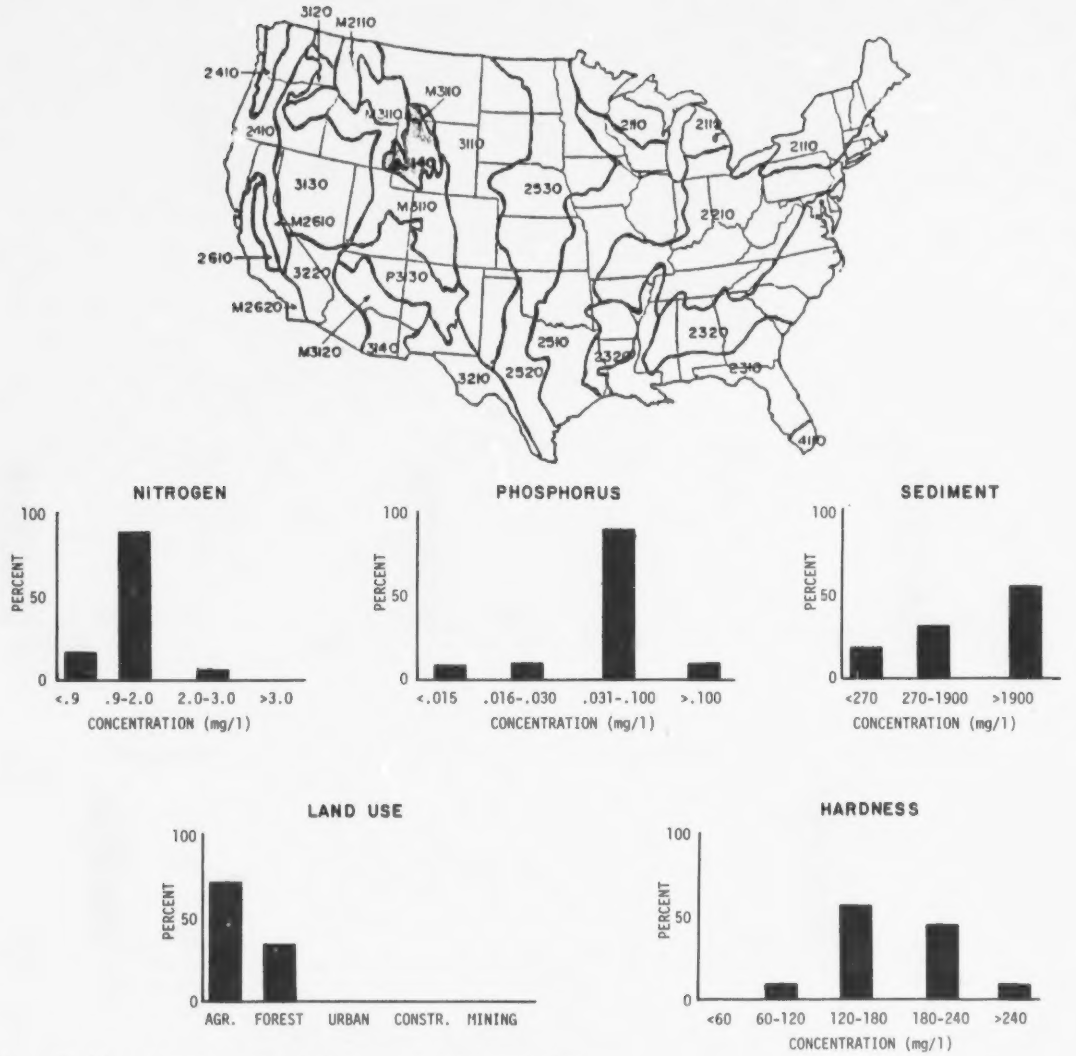


Fig. 5.24. Province A3140 - WYOMING BASIN

The Wyoming Basin covers 42,300 mi^2 of western Wyoming. Temperatures average 4-11° C annually and precipitation of 125-300 mm yearly is fairly evenly distributed throughout the year. Sagebrush and aridisols are found in the Basin.

Nitrogen: 86% of the streams have medium concentrations

Phosphorus: 90% of the streams have high concentrations

Sediment: High concentrations in 48% of the streams; 30% medium concentrations

Land Use: 67% agriculture (range)

Hardness: Hard water

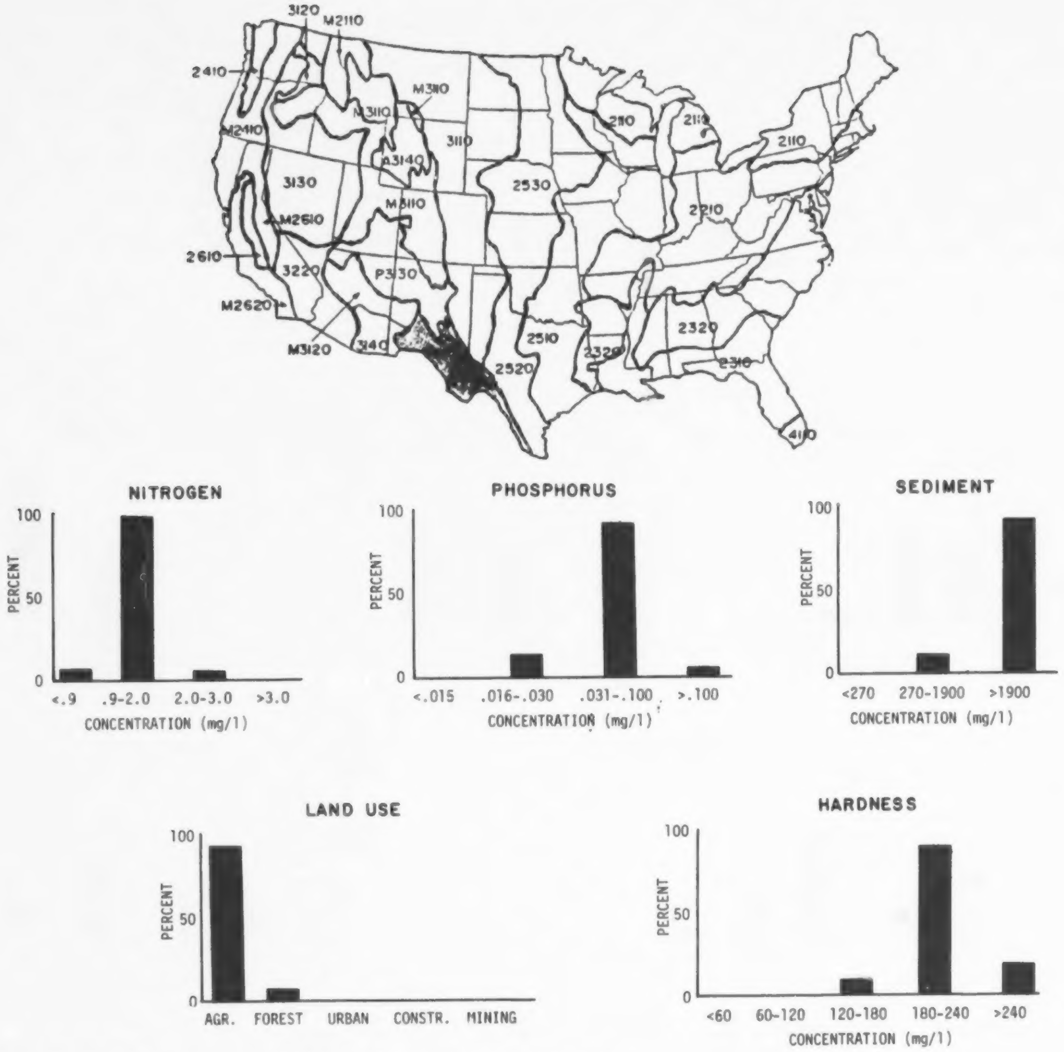


Fig. 5.25. Province 3210 - CHIHUAHUAN DESERT

The Chihuahuan Desert province is an area of 64,100 mi^2 in southwestern Texas and southern New Mexico. Average annual temperatures are 10-18° C and precipitation is less than 200 mm from local summer thunderstorms. Aridisols and entisols are the dominant soils and thorny shrub is the dominant vegetation.

Nitrogen: 97% of the rivers have medium concentrations

Phosphorus: 90% of the rivers have high concentrations

Sediment: 85% of the rivers with high concentrations

Land Use: 95% agriculture (range)

Hardness: Hard water

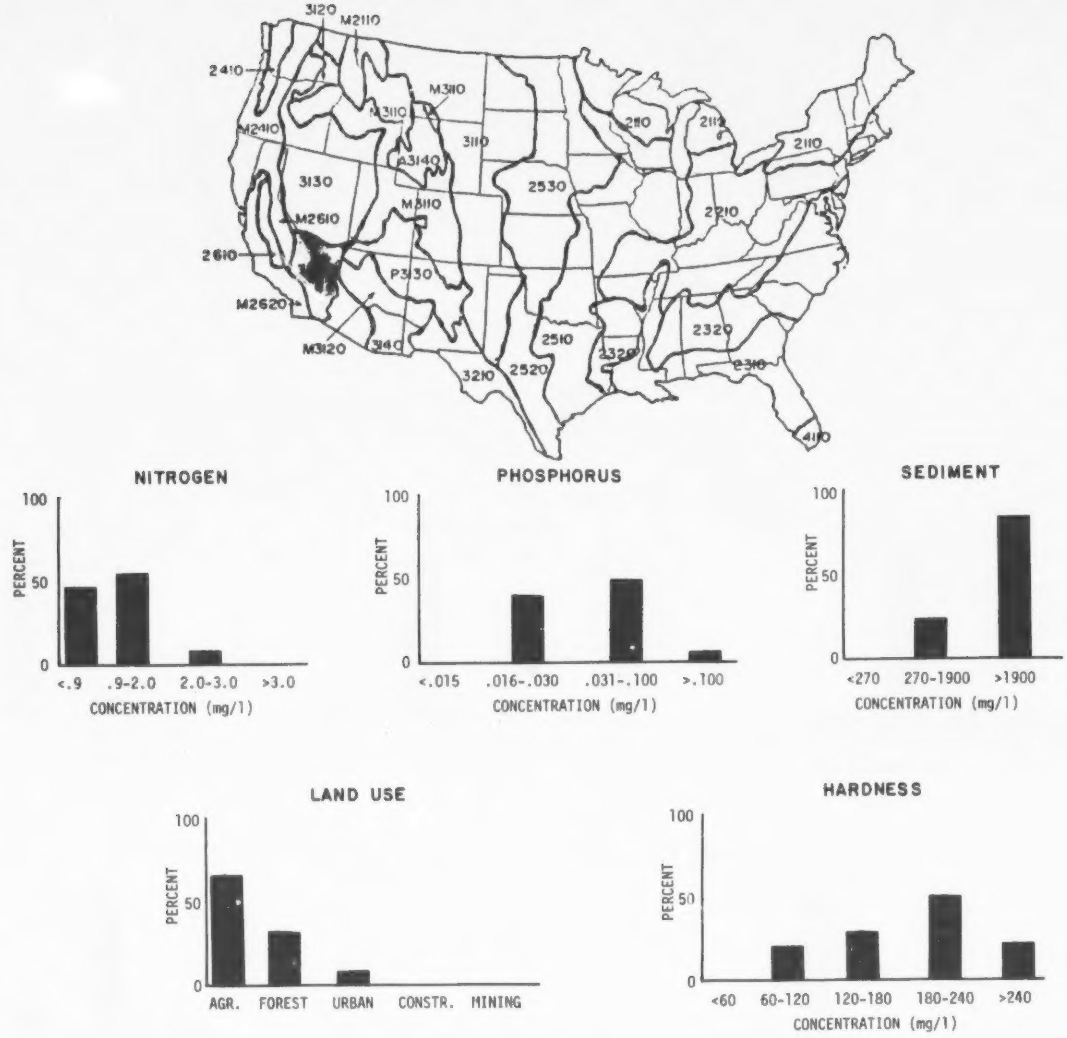


Fig. 5.26. Province 3220 - AMERICAN DESERT

The American Desert (77,500 mi^2) is composed of the Mojave, Colorado, and Sonoran Deserts of southern Nevada, southeastern California, and southwestern Arizona. This arid region has average annual temperatures of 15-25° C. Precipitation, from winter and summer thunderstorms, is 5-250 mm in valleys and up to 610 mm in mountains. Cacti and thorny shrub, and aridisols and entisols are found in these deserts.

Nitrogen: Low and medium concentrations; 59% of streams medium

Phosphorus: Primarily medium and high (60% of streams) concentrations

Sediment: 70% of the rivers with high, remainder with medium concentrations

Land Use: 68% agriculture (range)

Hardness: 75% of streams with hard water

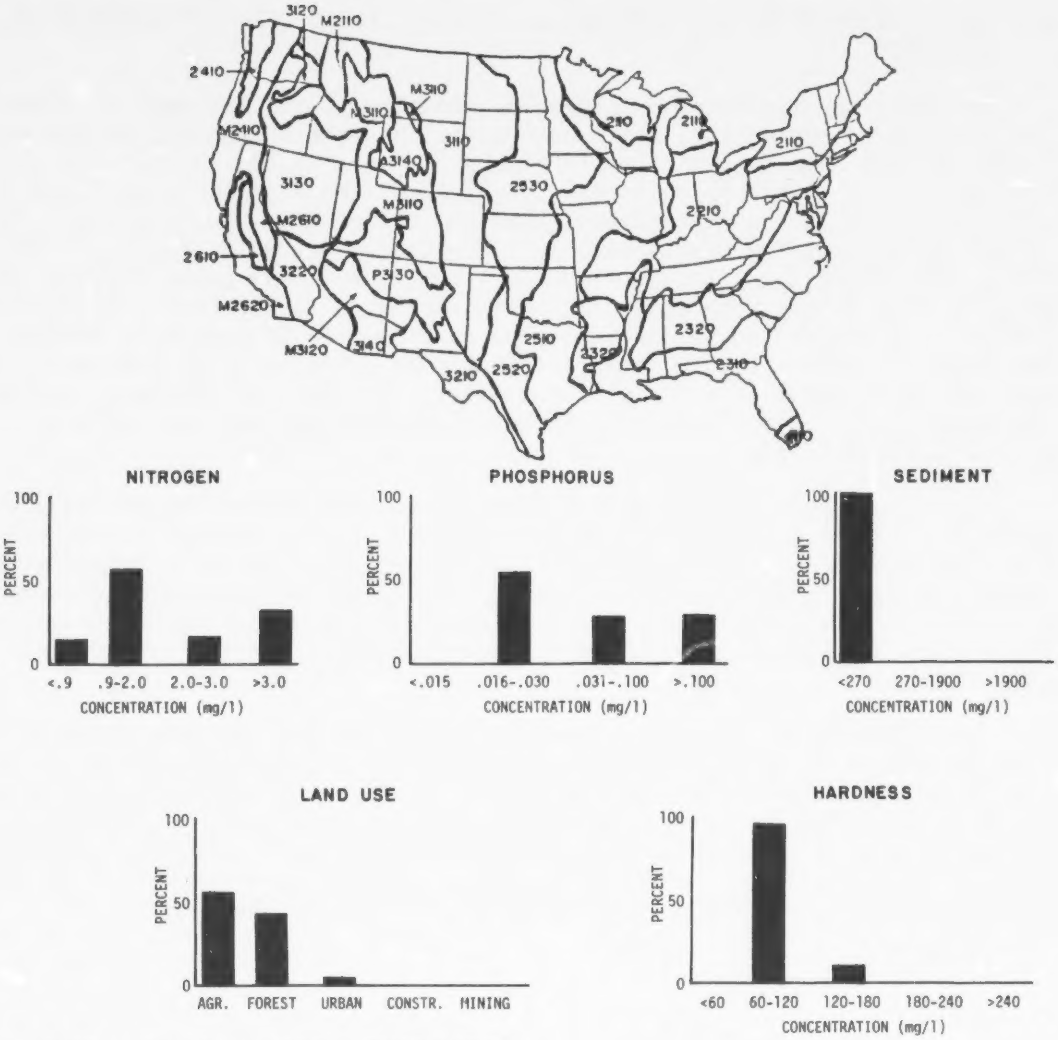


Fig. 5.27. Province 4110 - EVERGLADES

The small Everglades province of 7,800 mi^2 in southern Florida south of Lake Okeechobee is the only humid tropical area in the continental United States. The area has an average annual temperature of 21-24° C and precipitation of 1270-1650 mm yearly mainly in late spring to mid-autumn. Open marsh and tropical moist hardwoods are the dominant vegetation and histosols and inceptisols the dominant soils.

Nitrogen: Medium (58% of the streams) to high concentrations

Phosphorus: Medium (61% of the streams) to high concentrations

Sediment: All streams with low sediment concentrations

Land Use: 57% agriculture

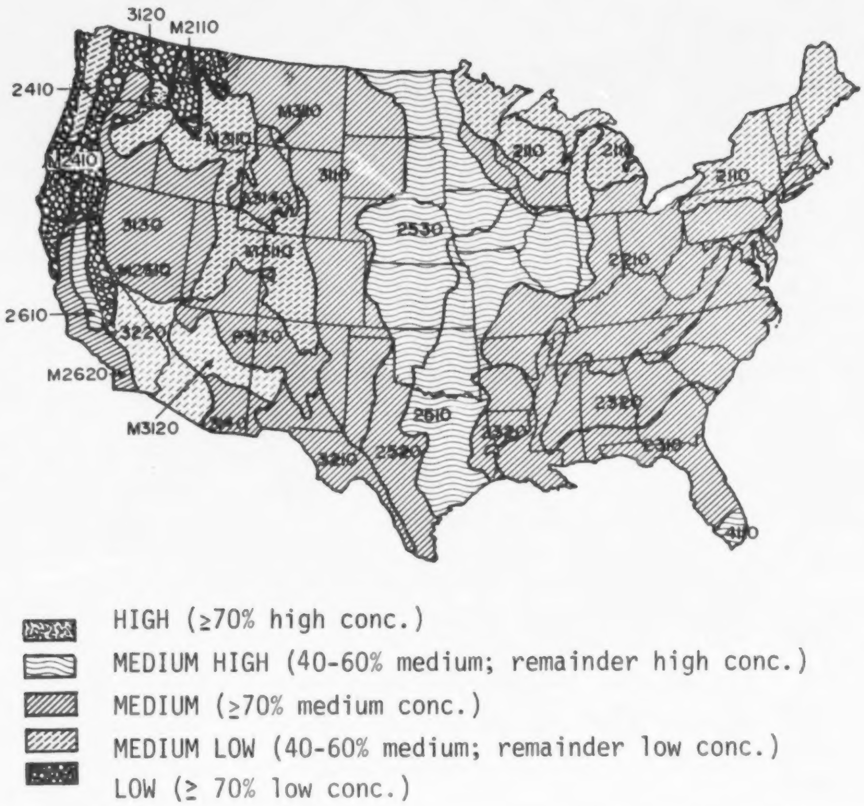
Hardness: 95% of the streams medium hard

5.5 ANALYSIS OF NITROGEN, PHOSPHORUS, SEDIMENT, LAND USE, AND HARDNESS BY PROVINCE

In order to determine how nitrogen, phosphorus, and sediment in rivers are distributed regionally, their concentrations were determined by province, tabulated, and mapped by similarity (Table 5.1, Fig. 5.28 - 5.30). The concentration levels used for nitrogen, phosphorus, and sediment are: "Low" ≥ 70% of streams have low concentrations; "Medium Low" generally 40 - 60% have medium concentrations and the rest have mainly low concentrations; "Medium" ≥ 70% have medium concentrations; "Medium High" 40 - 60% have medium concentrations and the rest have mainly high concentrations; and "High" ≥ 70% have high concentrations. Land use and hardness also were determined by province, tabulated, and mapped by similarity to show distributional patterns (Fig. 5.31 and 5.32). Associations between nitrogen and phosphorus; sediment and nitrogen; sediment and phosphorus; and sediment, phosphorus, and nitrogen were tabulated and mapped (Table 5.2, Fig. 5.33 - 5.36).

Land use correlations with sediment, phosphorus, and nitrogen concentrations in rivers also were analyzed and are presented in tabular and mapped form (Table 5.3; Fig. 5.37 - 5.39). Land use modifies the terrain and alters natural runoff of sediment and nutrients. For example, in heavy agricultural areas of the United States agricultural chemical loadings into rivers are high. The dry areas of the Southwest are considered rangeland which is included as agriculture in this analysis.

The analysis of sediment, nitrogen, and phosphorus concentrations by province demonstrates regional patterns as shown in succeeding figures. Several trends have emerged in the analysis of nitrogen, phosphorus, and sediment; in the interaction of these elements; and in the association of land use with nitrogen, phosphorus, and sediment. Also, broad patterns of the association of land use and sediment, phosphorus, and nitrogen have emerged showing that land use is a concentration determinant at a broad regional level.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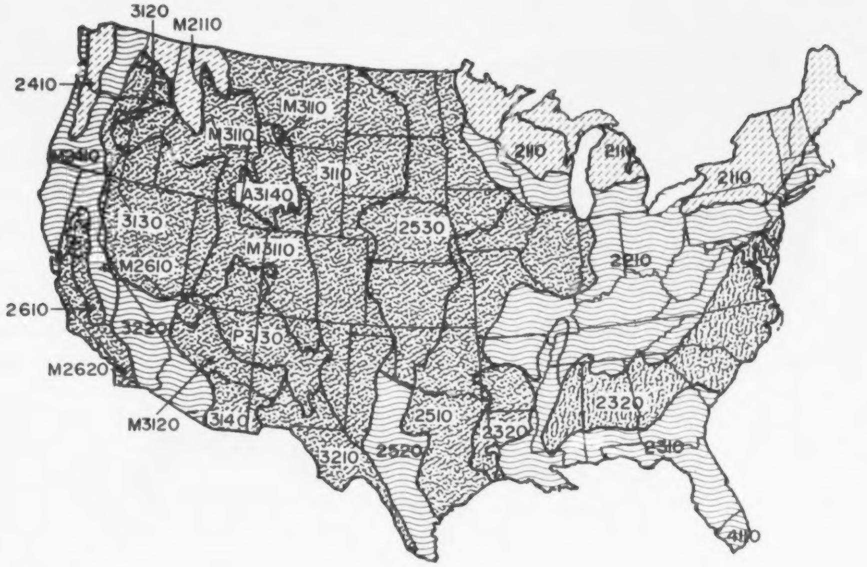
3210
2520
2310
410

▨ HIGH (≥70% high conc.)
▨ MEDIUM HIGH (40-60% medium; remainder high conc.)
▨ MEDIUM (≥70% medium conc.)
▨ MEDIUM LOW (40-60% medium; remainder low conc.)
▨ LOW (≥ 70% low conc.)

Fig. 5.28. Nitrogen concentrations in rivers of the United States by province. (See also Table 5.1.)

NITROGEN

Concentrations of nitrogen in rivers in the United States are predominantly medium to low. Ten provinces encompassing most of the eastern United States and most of the lowland provinces of the Steppe Region (Domain 3000) have medium concentrations of nitrogen in their streams. Medium low and low concentrations dominate the rivers of the Great Lakes/Northeast United States, the Pacific Northwest, the Rocky Mountain Province and a portion of the Southwestern desert area. High and medium high nitrogen concentrations are associated with the heavy agricultural use areas of the Midwest, south Florida, Palouse Grassland, and California's Central Valley.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2610
3220
P3130
M2620
M3120
3140
2510
2320
2320
2520
3210
2310
4110

▩ HIGH (≥70% high conc.)

▤ MEDIUM HIGH (40-60% medium; remainder high conc.)

▨ MEDIUM (≥70% medium conc.)

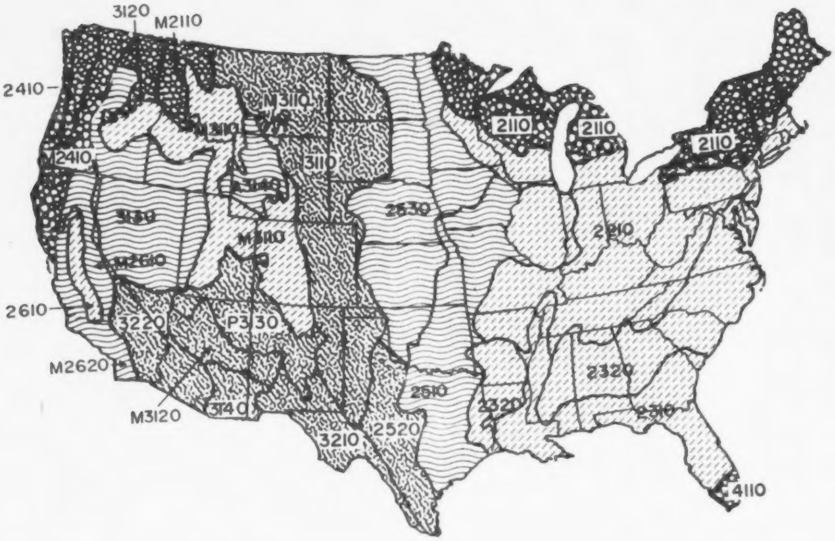
▨ MEDIUM LOW (40-60% medium; remainder low conc.)

▩ LOW (≥70% low conc.)

Fig. 5.29. Phosphorus concentrations in rivers of the United States by province. (See also Table 5.1.)

PHOSPHORUS

Generally, high concentrations of phosphorus are found in rivers of the United States. Similarity of phosphorus distribution is shown clearly by the strong clustering of provinces with medium high and high concentrations. Fourteen provinces, mainly in the Midwest and Steppe Domain (3000) have high concentrations of phosphorus in their rivers. Seven provinces in various areas of the country have medium high concentrations of phosphorus. Phosphorus inputs are derived primarily from natural sources in the West and Florida, and agricultural runoff in most other regions. The Laurentian Mixed Forest (2110), Columbia Forest (M2110), and Willamette-Puget Forest (2410) have both low and high phosphorus concentrations, which probably is a result of urban and agricultural loading in localized areas.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2610
3220
P3130
M2620
2320
2510
2320
2310
M3120
3140
3210
2520
4110

▩ HIGH (≥70% high conc.)

▤ MEDIUM HIGH (40-60% medium; remainder high conc.)

▨ MEDIUM (≥70% medium conc.)

▧ MEDIUM LOW (40-60% medium; remainder low conc.)

▦ LOW (≥70% low conc.)

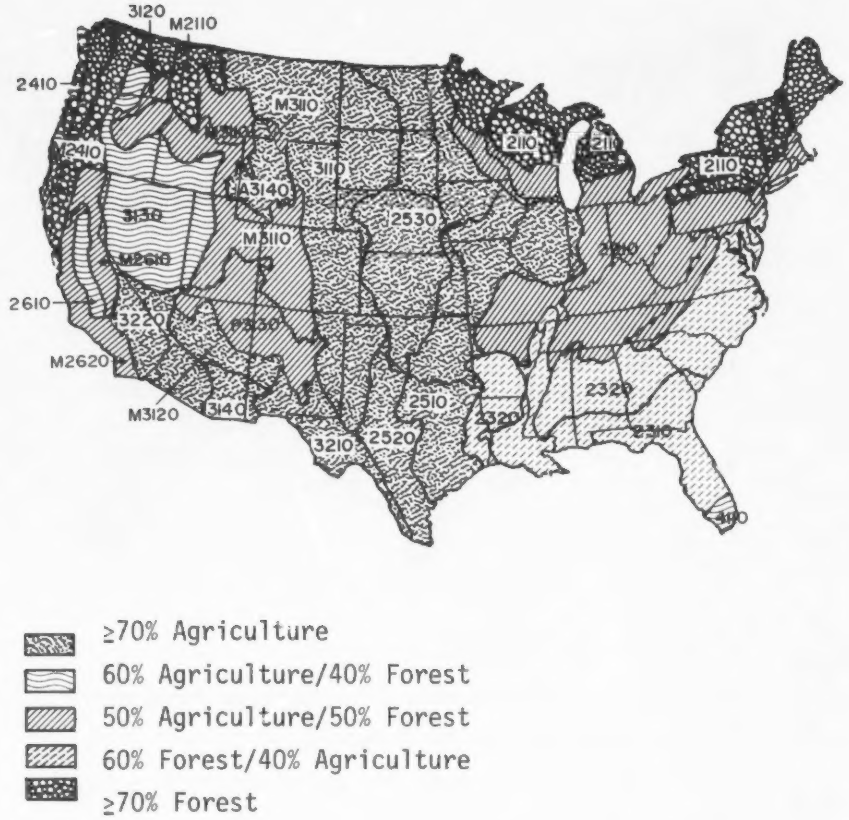
Fig. 5.30. Sediment concentrations in rivers of the United States by province. (See also Table 5.1.)

SEDIMENT

Sediment concentrations in rivers of the United States are distributed from low to high and provinces with similar concentrations are clumped in distinct areas. From five to seven provinces show similarities in concentration categories. Sediment generally is found in low concentrations in the rivers of the Great Lakes, the Northeast, and the Pacific Northwest. Medium to low concentrations occur throughout most of the East and in the Rocky Mountains. High concentrations are found in the Southwest and Great Plains and medium high concentrations in the Midwest, Great Basin, Wyoming Basin, and upland California. Provinces with high sediment concentrations in the rivers are those with highly erodible soil and intermittant flow. Those with medium high sediment concentrations are in areas of highly erodible soil or heavy agriculture.

Table 5.1. Provinces showing similarity in concentrations of nitrogen, phosphorus, and sediment in rivers. Categories determined by dominant levels of concentration. "Low - ≥ 70 percent of streams have low concentrations; "Medium Low" - generally 40-60 percent have medium levels and the rest have mainly low concentrations; "Medium" - ≥ 70 percent have medium concentrations; "Medium High" - 40-60 percent have medium levels and the rest have high; and "High" - ≥ 70 percent have high concentrations. Numbers are province designations.

	Low	Medium Low	Medium	Medium High	High
Nitrogen	M2110 M2410 M2610	2110 2410 M3110 M3120 3220	2210 2310 2320 M2620 3110 3130 P3130 3140 A3140 3210	2510 2530 2610 4110	3120
Phosphorus	-	-	-	2210 2310 M2410 2520 M2610 3220 4110	2320 2510 2530 2610 M2620 3110 M3110 3120 M3120 3130 P3130 3140 A3140 3210
	(Provinces 2110, 2410, and M2110 have 40-50 percent of streams with low concentrations and 40-50 percent with high concentrations.)				
Sediment	2110 M2110 2410 M2410 3120 4110	2210 2310 2320 2610 M3110		2510 2530 M2620 M2610 3130 A3140	2520 3110 M3120 P3130 3140 3210 3220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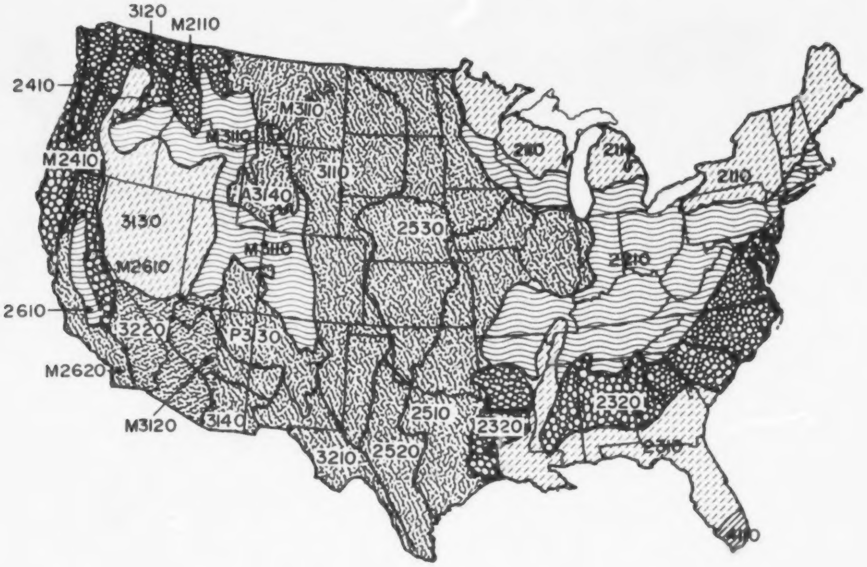
M2620
M3120
3140
2510
3210
2520
2320
2310
2110
2110
2110
4110
▨ ≥70% Agriculture
▤ 60% Agriculture/40% Forest
▨ 50% Agriculture/50% Forest
▨ 60% Forest/40% Agriculture
▩ ≥70% Forest

Fig. 5.31. Land use, i.e., agriculture and forest, throughout the United States by province.

LAND USE

Land use is divided into agriculture (including range) and forest for this comparison, and is separated into five classes-≥70% agriculture, ≥70% forest, 50% agriculture and 50% forest, 60% agriculture and 40% forest, and 40% agriculture and 60% forest. Land alteration is an important modifier of surface runoff and consequently affects loading of sediment and nutrients. Provinces with dominant land use either agricultural or forest are clustered. Nine provinces have greater than 70 percent of the land in agriculture. The Midwest, with high row crop and grain production, and the southwest, with rangeland dominant are the major high agricultural areas of the country. The major forested areas of the country are the Great Lakes/Northeast and the Pacific Northwest with ≥70% of the land forested.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P3130
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2320
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M3120
3140
3210
2520
2310
4110

▩ HARD (≥70% hard water)

▤ MEDIUM HARD (40-60% medium; remainder hard water)

▨ MEDIUM (≥70% medium hard water)

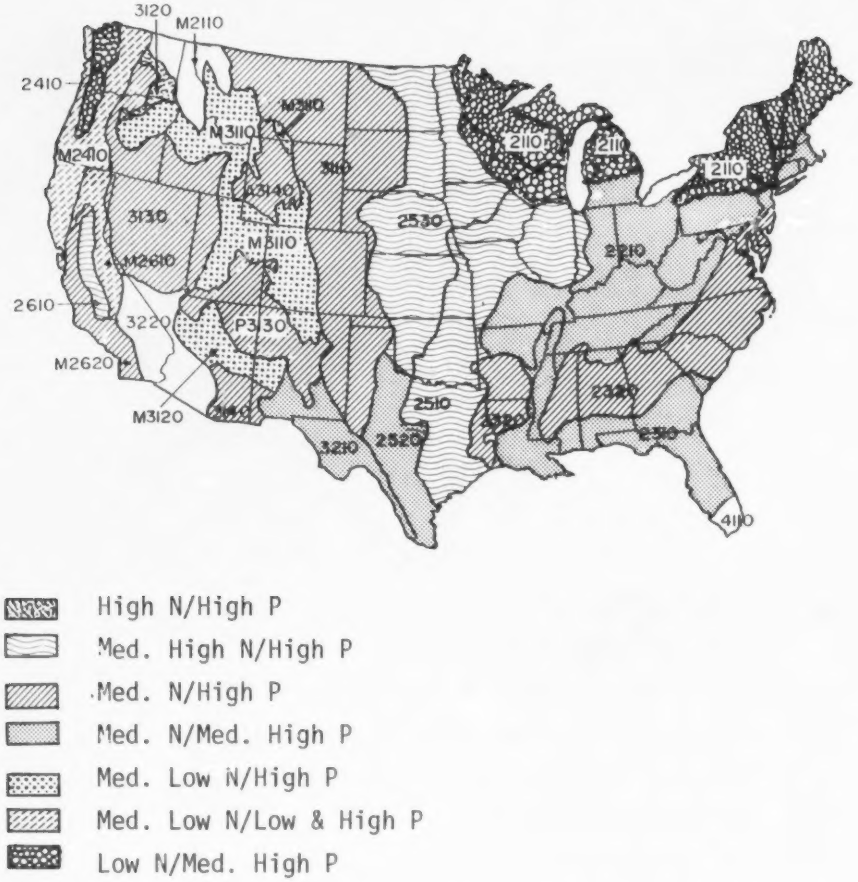
▧ MEDIUM SOFT (40-60% medium; remainder soft water)

▦ SOFT (≥70% soft water)

Fig. 5.32. Hardness, as $CaCO_3$ concentration, in rivers of the United States by province.

HARDNESS

Hard water, as measured by $CaCO_3$, dominates the midwestern and the southwestern portions of the United States. Eleven provinces have waters considered hard, i.e., ≥70 percent of the rivers with water at the high concentration level of $CaCO_3$. Soft water, or low $CaCO_3$ concentrations, and medium soft waters, are found in the Southeast, Great Lakes/Northeast area, and Pacific Northwest.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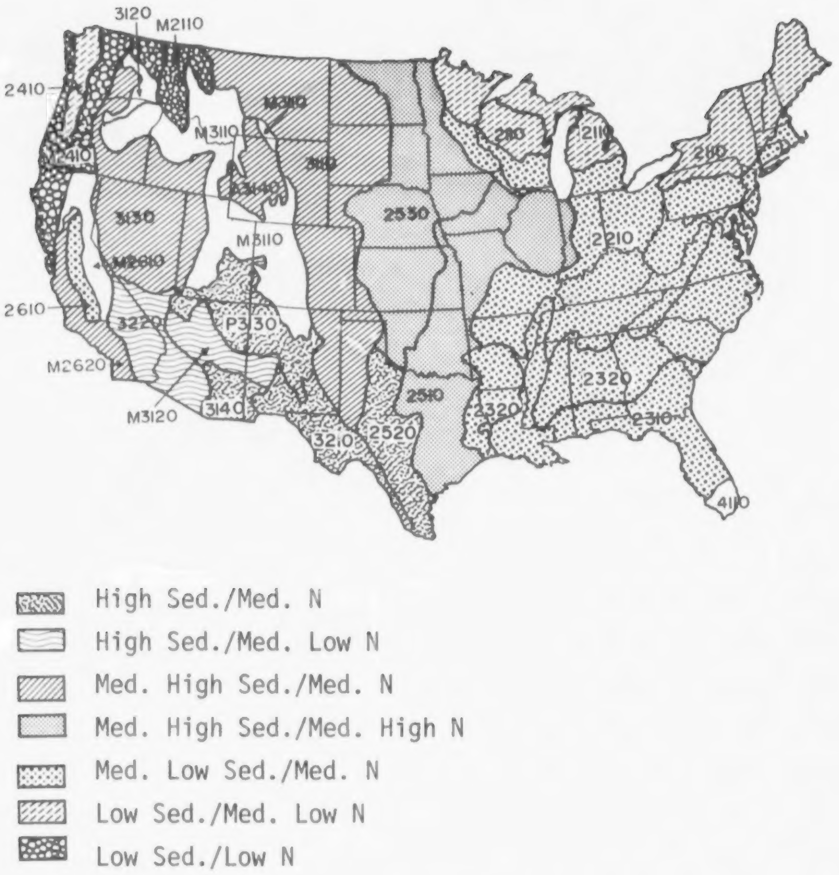
2520
2320
2310
4110
High N/High P
Med. High N/High P
Med. N/High P
Med. N/Med. High P
Med. Low N/High P
Med. Low N/Low & High P
Low N/Med. High P

Fig. 5.33. Province similarities in nitrogen and phosphorus concentrations in rivers of the United States. (See also Table 5.2.)

NITROGEN/PHOSPHORUS

Province similarity in nitrogen and phosphorus are most prevalent in the Steppe Domain (3111) with eight provinces having predominantly high phosphorus and medium nitrogen concentrations. Three provinces in the agricultural areas of the Midwest and the California Valley have high phosphorus and medium high nitrogen concentrations. Another agricultural area, the Palouse Grassland, has high phosphorus and high nitrogen concentrations in the streams. Undesignated provinces on the map are identified in Table 5.5.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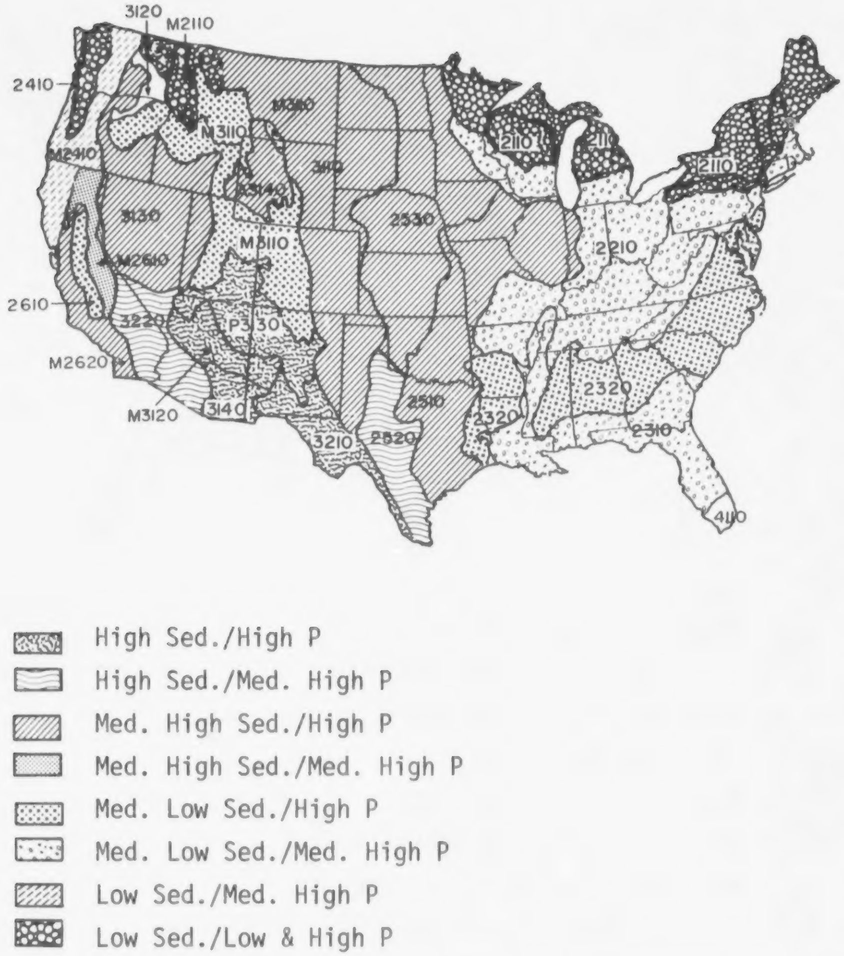
▨ High Sed./Med. N
▤ High Sed./Med. Low N
▨ Med. High Sed./Med. N
▢ Med. High Sed./Med. High N
▦ Med. Low Sed./Med. N
▨ Low Sed./Med. Low N
▩ Low Sed./Low N

Fig. 5.34. Province similarities in sediment and nitrogen concentrations in rivers of the United States. (See also Table 5.2.)

SEDIMENT/NITROGEN

High sediment and medium nitrogen are found in four provinces in the Southwest. Medium high sediment is coupled with medium high nitrogen in four provinces in the Midwest and with medium nitrogen in the Steppe Domain and in the California coastal uplands. High sediment does not suggest high nitrogen always. Provinces with low sediment may have low (M2110 or M2410) or high (3120) nitrogen and provinces with high sediment may have medium (2520) or medium low (3220) sediment. Undesignated provinces on the map are identified in Table 5.2.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2320
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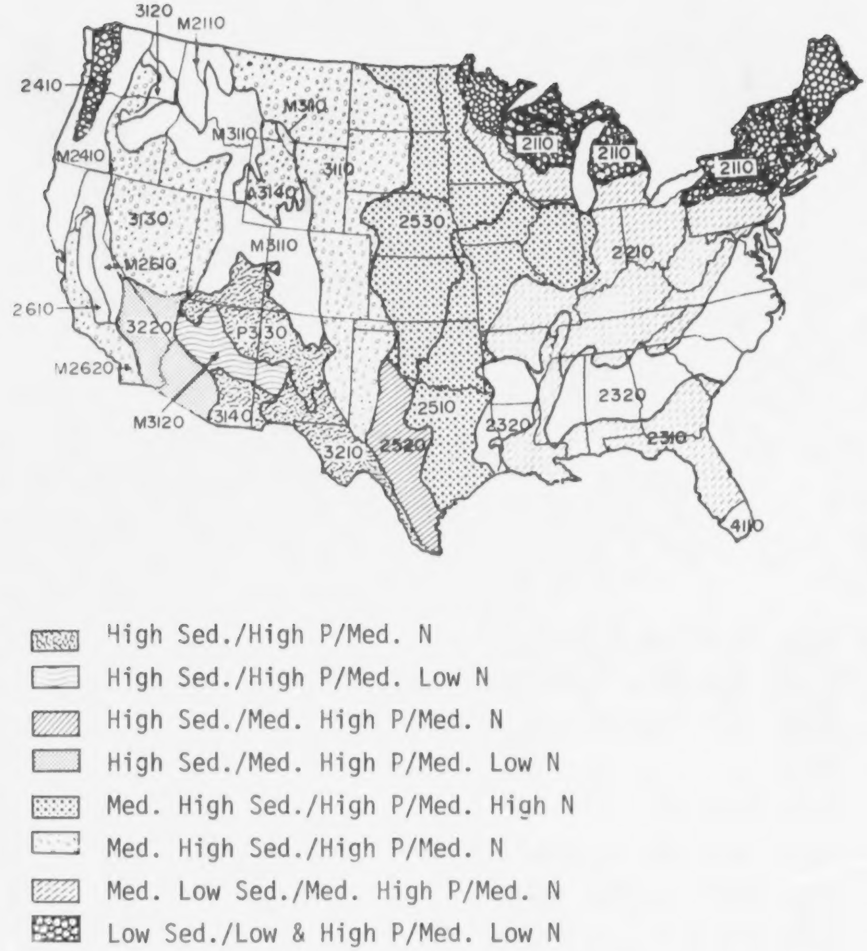
3210
3140
M3120
2310
4110
High Sed./High P
High Sed./Med. High P
Med. High Sed./High P
Med. High Sed./Med. High P
Med. Low Sed./High P
Med. Low Sed./Med. High P
Low Sed./Med. High P
Low Sed./Low & High P

Fig. 5.35. Province similarities in sediment and phosphorus concentrations in rivers of the United States. (See also Table 5.2.)

SEDIMENT/PHOSPHORUS

Strong correlations exist between sediment and phosphorus concentrations. High or medium high sediment shows in high or medium high phosphorus concentrations in 13 provinces comprising about half the land mass of the United States. Correlation between sediment, phosphorus, and land use is evident here because these are all agriculture or range areas. Naturally high phosphorus levels are confirmed for the Southwest. Low sediment and low and high phosphorus concentrations are found in the Pacific Northwest. In a few isolated areas, low sediment is correlated with high (3120) phosphorus or medium high phosphorus concentrations (M2410 and 4110).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M2620
M3120
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2110
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4110
▩ High Sed./High P/Med. N
▭ High Sed./High P/Med. Low N
▨ High Sed./Med. High P/Med. N
▭ High Sed./Med. High P/Med. Low N
▦ Med. High Sed./High P/Med. High N
▭ Med. High Sed./High P/Med. N
▨ Med. Low Sed./Med. High P/Med. N
▩ Low Sed./Low & High P/Med. Low N

Fig. 5.36. Province similarities in sediment, phosphorus, and nitrogen concentrations in rivers of the United States. (See also Table 5.2.)

SEDIMENT/PHOSPHORUS/NITROGEN

The comparison of sediment, phosphorus, and nitrogen at the five concentration levels (high, medium high, medium, medium low, low) resulted in 125 possible combinations. Few patterns showing relations between sediment, phosphorus, and nitrogen were observed. Four provinces emerged having medium high sediment, high phosphorus, and medium nitrogen. High sediment, high phosphorus, and medium nitrogen are found in three southwestern provinces and a fourth southwestern province has the same sediment and phosphorus, but medium low nitrogen. The Great Lakes/Northeast and Pacific Northwest were similar as was the Midwest. Undesignated provinces on the map are identified in Table 5.2.

Table 5.2. Provinces showing similarity in concentrations of nitrogen and phosphorus, sediment and nitrogen, sediment and phosphorus, phosphorus and sediment and nitrogen. Categories determined by dominant levels of concentration, i.e., low - ≥ 70% of streams have low concentrations; medium low - generally 40-60% have medium concentrations and the rest have mainly low concentrations; medium - ≥ 70% have medium concentrations; medium high - 40-60% have medium concentrations and the rest have high; and high - ≥ 70% have high concentrations. Provinces are designated by numbers.

Nitrogen and Phosphorus

Correlation	Province
High N & High P	3120
Med. High N & High P	2510, 2530, 2610
Med. High N & Med. High P	4110
Med. N & High P	2320, M2620, 3110, 3130, P3130, 3140, A3140, 3210
Med. N & Med. High P	2210, 2310, 2520
Med. Low N & High P	M3110, M3120
Med. Low N & Med. High P	3220
Med. Low N & Low & High P	2110, 2410
Low N & Med. High P	M2410, M2610
Low N & Low & High P	M2110

Sediment and Nitrogen

Correlation	Province
High Sed. & Med. N	2520, P3130, 3140, 3210
High Sed. & Med. Low N	M3120, 3220
Med. High Sed. & Med.High N	2510, 2530
Med. High Sed. & Med. N	M2620, 3110, 3130, A3140
Med. High Sed. & Low N	M2610
Med. Low Sed. & Med. High N	2610
Med. Low Sed. & Med. N	2210, 2310, 2320
Med. Low Sed. & Med. Low N	M3110
Low Sed. & High N	3120
Low Sed. & Med. High N	4110
Low Sed. & Med. Low N	2110, 2410
Low Sed. & Low N	M2110, M2410

Table 5.2 (Continued).

Sediment and Phosphorus

Correlation	Province
High Sed. & High P	M3120, P3130, 3140, 3210
High Sed. & Med. High P	2520, 3220
Med. High Sed. & High P	2510, 2530, M2620, 3110, 3130, A3140
Med. High Sed. & Med. High P	M2610
Med. Low Sed. & High P	2320, 2610, M3110
Med. Low Sed. & Med. High P	2210, 2310
Low Sed. & High P	3120
Low Sed. & Med. High P	M2410, 4110
Low Sed. & Low & High P	2110, M2110, 2410

Sediment, Phosphorus, and Nitrogen

Correlation	Province
High Sed. & High P & Med. N	P3130, 3140, 3210
High Sed. & High P & Med. Low N	M3120
High Sed. & Med. High P & Med. N	2520
High Sed. & Med. High P & Med. Low N	3220
Med. High Sed. & High P & Med. High N	2510, 2530
Med. High Sed. & High P & Med. N	M2620, 3110, 3130, A3140
Med. High Sed. & Med. High P & Low N	M2610
Med. Low Sed. & High P & Med. High N	2610
Med. Low Sed. & High P & Med. N	2320
Med. Low Sed. & High P & Med. Low N	M3110
Med. Low Sed. & Med. High P & Med. N	2210, 2310
Low Sed. & High P & High N	3120
Low Sed. & Med. High P & Med. High N	4110
Low Sed. & Med. High P & Low N	M2410
Low Sed. & Low & High P & Med. Low N	2110, 2410
Low Sed. & Low & High P & Low N	M2210

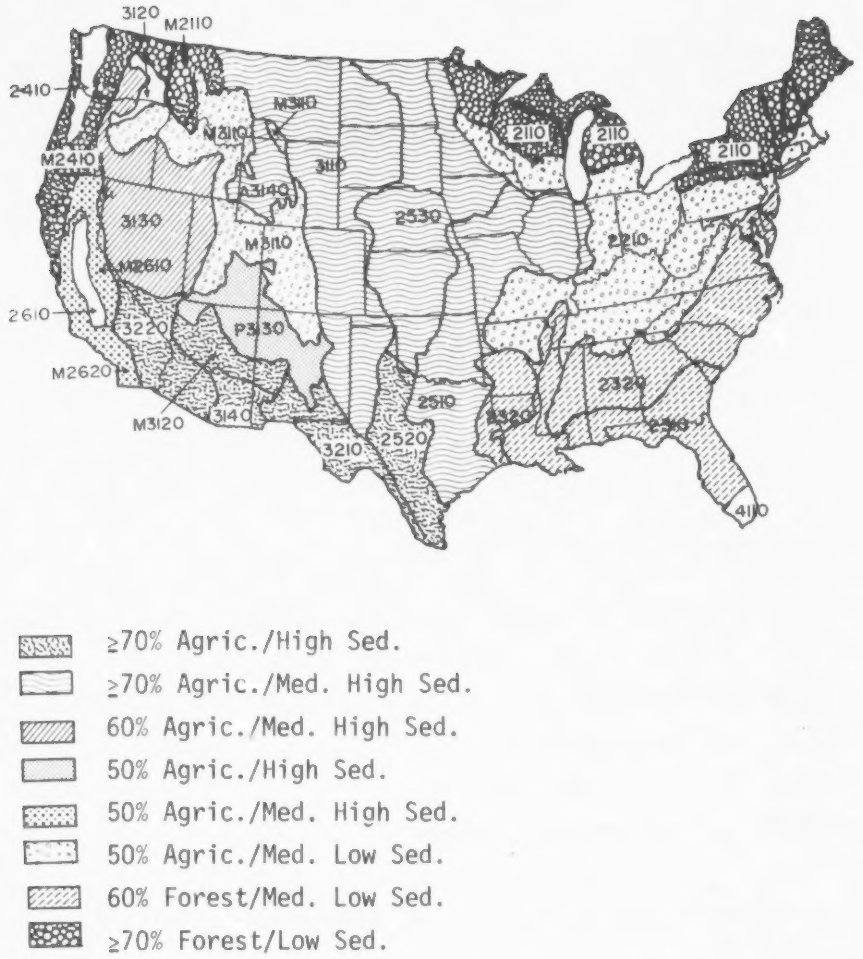
3120
M2110
2410
M2410
M3110
M3110
3110
A3140
3130
M3110
M2610
2610
3220
P3130
M2620
M3120
3140
3210
2520
2510
2530
2110
2110
2110
2210
2320
2320
4110
≥70% Agric./High Sed.
≥70% Agric./Med. High Sed.
60% Agric./Med. High Sed.
50% Agric./High Sed.
50% Agric./Med. High Sed.
50% Agric./Med. Low Sed.
60% Forest/Med. Low Sed.
≥70% Forest/Low Sed.

Fig. 5.37. Province similarities in land use and sediment concentrations in rivers of the United States. (See also Table 5.3.)

LAND USE/SEDIMENT

A high percentage (≥70%) of agriculture, primarily rangeland, is correlated with high sediment concentration in the Southwest and with medium high sediment concentrations in the Midwest and Great Plains. A high percentage of forested land (≥70%) is correlated with low sediment concentration in the Great Lakes/Northeast area and Pacific Northwest. Medium low sediment is correlated with 60% forest in the Southeast. Undesignated provinces on the map are identified in Table 5.3.

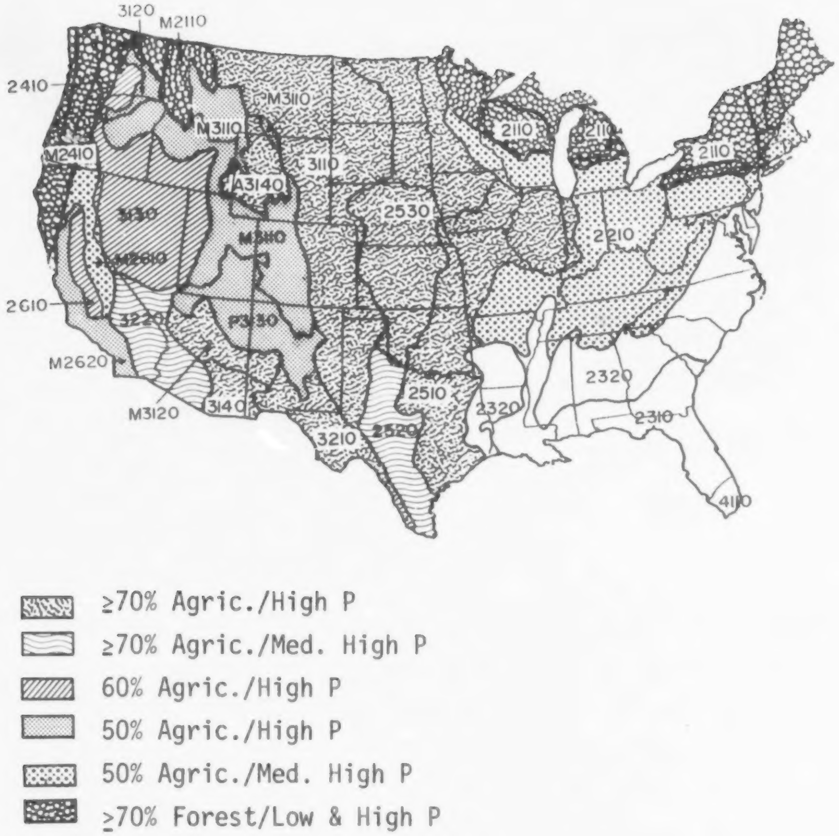
3120
M2110
2410
M3110
M3110
M2410
3110
A3140
2530
2110
2110
2110
2210
3130
M3110
M2610
2610
3220
P3130
M2620
2510
2320
2320
2310
M3120
3140
3210
2520
4110
▨ ≥70% Agric./High P
▤ ≥70% Agric./Med. High P
▨ 60% Agric./High P
▨ 50% Agric./High P
▨ 50% Agric./Med. High P
■ ≥70% Forest/Low & High P

Fig. 5.38. Province similarities in land use and phosphorus concentrations in rivers of the United States. (See also Table 5.3.)

LAND USE/PHOSPHORUS

A high percentage of agricultural land (≥70%) is correlated with high phosphorus concentrations in seven provinces in the Midwest and Southwest and with medium high phosphorus in two southwestern provinces. Two provinces have 60% agriculture and high phosphorus. Areas of 50% agriculture also have high and medium high phosphorus concentrations in rivers. A high percentage of forest (≥70%) is correlated with low and high phosphorus in the Great Lakes/Northeast area, and the Pacific Northwest. Other correlations between land use and phosphorus are shown in Table 5.3.

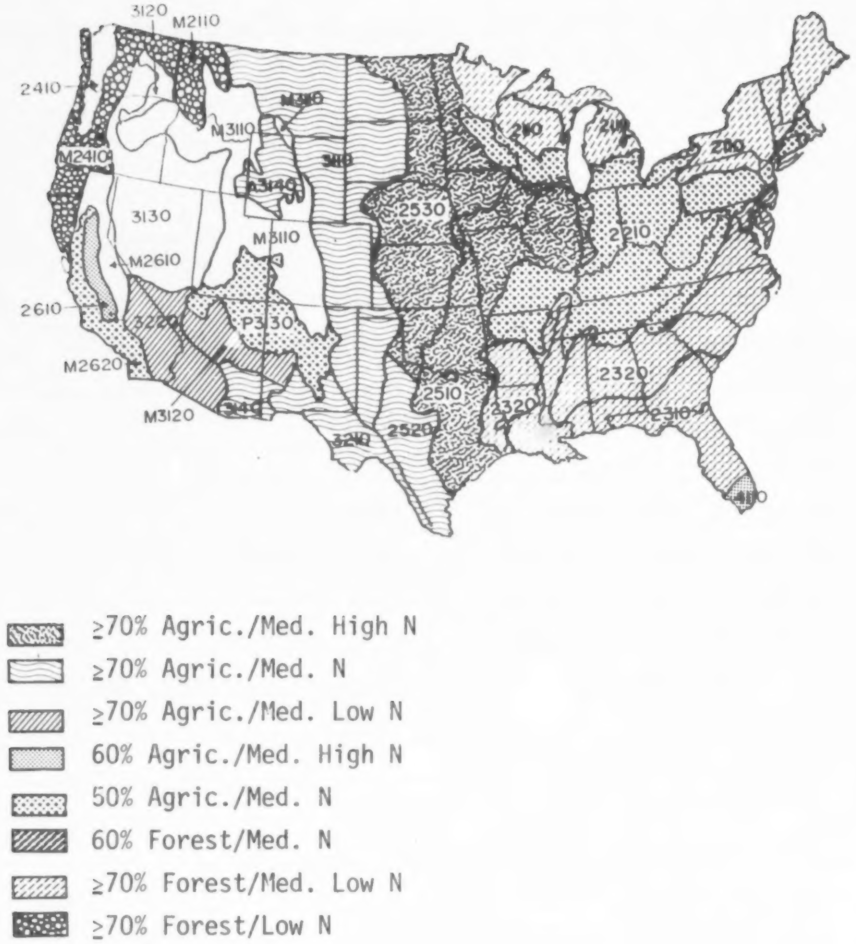
3120
M2110
2410
M2410
M3110
3110
3130
M3110
M2610
2610
3220
P3130
M2620
M3120
2530
2210
2510
2520
3210
2320
2320
2310
≥70% Agric./Med. High N
≥70% Agric./Med. N
≥70% Agric./Med. Low N
60% Agric./Med. High N
50% Agric./Med. N
60% Forest/Med. N
≥70% Forest/Med. Low N
≥70% Forest/Low N

Fig. 5.39. Province similarities in land use and nitrogen concentrations in rivers of the United States. (See also Table 5.3.)

LAND USE/NITROGEN

Fewer provinces show direct correlations between land use and nitrogen. Areas with a high percentage of agricultural land are correlated with medium high nitrogen concentrations in two provinces in the Midwest and with medium nitrogen concentrations in five provinces primarily in the eastern Steppe Domain. Sixty percent agricultural use is correlated with medium high and medium nitrogen concentrations in the Southeast. A high percentage of forest and low or medium low nitrogen concentrations are found in the Great Lakes/Northeast region and the Pacific Northwest. Undesignated areas on the map are identified in Table 5.3.

Table 5.3. Province similarities between land use and sediment, phosphorus, and nitrogen concentrations in streams.

Land Use and Sediment

Correlation	Province
≥70% Agric./High Sed.	2520, M3120, 3140, 3210, 3220
≥70% Agric./Med. High Sed.	2510, 2530, 3110, A3140
60% Agric./Med. High Sed.	3130
60% Agric./Med. Low Sed.	2610
60% Agric./Low Sed.	4110
50% Agric./High Sed.	P3130
50% Agric./Med. High Sed.	M2610, M2620
50% Agric./Med. Low Sed.	2210, M3110
60% Forest/Med. Low Sed.	2310, 2320
≥70% Forest/Low Sed.	2110, M2110, 2410, M2410

Land Use and Phosphorus

Correlation	Province
≥70% Agric./High P	2510, 2530, 3110, M3120, 3140, A3140, 3210
≥70% Agric./Med. High P	2520, 3220
60% Agric./High P	2610, 3130
60% Agric./Med. High P	4110
50% Agric./High P	M2620, M3110, 3120, P3130
50% Agric./Med. High P	2210, M2610
60% Forest/High P	2320
60% Forest/Med. High P	2310
≥70% Forest/Med. High P	M2410
≥70% Forest/Low & High P	2110, M2110, 2410

Table 5.3 (Continued).

Land Use and Nitrogen

Correlation	Province
≥70% Agric./Med. High N	2510, 2530
≥70% Agric./Med. N	2520, 3110, 3140, A3140, 3210
≥70% Agric./Med. Low N	M3120, 3220
60% Agric./Med. High N	4110, 2610
60% Agric./Med. N	3130
50% Agric./High N	3120
50% Agric./Med. N	2210, 2610, P3130
50% Agric./Med. Low N	M3110
50% Agric./Low N	M2610
60% Forest/Med. N	2310, 2320
≥70% Forest/Med. Low N	2110, 2410
≥70% Forest/Low N	M2110, M2410

5.6 CONCLUSIONS

A hierarchical plan has been presented that allows comparison of impacts of sediment and nutrients at different levels of resolution and provides an organizing model for research (Table 4.2). This scheme couples biological and geographical factors into an interactive system by treating each level of the hierarchy as an ecosystem. Each level of the hierarchy is nested into the level above it.

Bailey's Province ecoregion was used to determine how sediment, phosphorus, and nitrogen are distributed throughout the United States at the "regional" level of the hierarchy. Surface waters of the nation are not all different nor are they all similar in terms of concentrations of these factors. Nitrogen concentrations in rivers of the United States are predominantly low, phosphorus concentrations are predominantly high, and sediment concentrations vary from low to medium to high depending upon the region of the country. Sediment and phosphorus concentrations are correlated positively--high and medium sediment concentrations are correlated with high or medium phosphorus concentrations in approximately half of the land area of the United States. Sediment and nitrogen concentrations are not strongly correlated--high sediment correlates positively with high nitrogen only in areas of high agricultural use. Concentrations of phosphorus and sediment, and, to a lesser extent, nitrogen and sediment are associated with land use practices. The highly agricultural areas of the Midwest and Great Plains and the rangelands of the Southwest have high sediment and phosphorus concentrations in rivers. Highly forested areas, the Great Lakes/Northeast area and the Pacific Northwest, generally have low sediment and nitrogen concentrations in the rivers. Nitrogen and land use follow similar patterns but with fewer areas as strongly correlated.

General similarities among Province level ecosystems have emerged from these analyses and clearly show regional patterns. The similarity patterns are strongly correlated with land use practices and are clearly aggregated in major areas of the country.

1. The Laurentian Mixed Forest (2110), Columbia Forest (M2110), Willamette Puget Forest (2410), and Pacific Forest (M2410) usually are very similar in all factors analyzed. These provinces show the most consistent similarity which is probably due to their heavy forest covers and relatively low degree of agricultural development.

2. The Prairie Parkland (2510) and the Tall Grass Prairie (2530) are similar in concentration for each factor. Waters in this Midwest area are very similar and are influenced heavily by the agricultural practices of the region.

3. The Eastern Deciduous Forest (2210) and the Outer Coastal Plain Forest (2310) exhibit similarities in sediment and nutrient concentrations in streams. The Southeastern Mixed Forest (2320) is similar in some parameters to these two

provinces. In these provinces, forest is the climax vegetation, hence abandoned land or unused land will be forested and eventually will reduce sediment and nutrient levels in streams.

4. Strong provincial similarity is found in the Southwest. The Chihuahuan Desert (3210), American Desert (3220), Mexican Highlands Steppe (3140), Upper Gila Mountain Forest (M3120), Colorado Plateau (P3130), and to some extent the Prairie Brushland (2520) are similar for most factors. These are all desert lands, with irrigated agriculture and relatively sparse native vegetative cover, which is grazed as rangeland. The remainder of the Steppe Domain is variable. There is no consistent similarity in the lowlands or in the highlands. The Intermountain Sagebrush (3130) frequently is similar to the southwestern deserts, but is also similar to the Great Plains Short Grass Prairie (3110).

The California provinces are variable and show no consistent similarity within this region or with provinces in other areas.

These regional patterns do not aggregate consistently into Divisions of Bailey's ecoregion scheme. This inconsistency could be a result of lack of data, however it is more likely that land use practices, particularly agriculture, either override or the effects are enhanced by natural environmental factors that affect loading and concentrations of sediment and nutrients in surface waters. The Province category was adequate for this survey and should be retained for further verification of the regional scheme.

The data used here to show similarities is based upon surveys of rivers in somewhat restricted areas of the country. Similarities should be verified using existing data storage systems such as STORET or NAWDEX. There is need for verification particularly in the Southwest, Intermountain Basin, and the Southeastern Coastal Plain, because these areas had limited data for our analysis. Nutrient and sediment concentration data for lakes and reservoirs should be gathered to determine the general condition of these surface waters and to determine how well correlated concentrations are in standing and flowing waters.

There is a need for detailed study of sediment and nutrient concentrations and loadings in a typical river basin in dissimilar areas of the United States. A midwest basin with high sediment and nutrients and a Southeast or northwest area with lower sediment and nutrient concentrations and generally different land use practices should be compared. Such a comparison will also help refine the classification scheme developed in this study. This regional comparison should select a few physical and/or chemical parameters that could be used to provide a predictive method for determining the nature and extent of impacts to biota at a managerial level.

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CHAPTER 6

ASSESSMENT OF STRUCTURAL AND FUNCTIONAL BIOTIC VARIABLES AS MEASURES OF IMPACT IN FRESHWATERS

6.1 INTRODUCTION

Assessment of nutrient and sediment impacts in aquatic ecosystems requires 1) identification of ecosystem components and processes which respond, either directly or indirectly, to increased concentrations or fluxes of nutrients and sediment, and 2) measurement of component and process variables which reflect those responses. Components and processes can be identified at several levels of biological organization (Table 6.1), but, traditionally, interest has focused on lower levels (e.g., indicator organisms and commercially important species). Measurements of variables which reflect the physico-chemical nature of water and the state of biotic components have predominated. Recognition of causal interactions among biotic and abiotic components and of the dynamic nature of aquatic ecosystems is currently resulting in greater emphasis on process variables and higher levels of organization.

This chapter is an attempt to identify measurable variables which have been used or are of potential use in environmental impact analysis in aquatic (mostly freshwater) ecosystems. The variables considered are primarily biotic (see Ott 1978 for a discussion of abiotic variables and indices) and are arranged according to the hierarchical scheme developed in Chapter 4. For organizational purposes, a distinction is made between structural and functional variables. Structural variables are recognized as those which are measured instantaneously (measures of biotic state at a moment in time) and reflect static order. Functional variables are recognized as those which are measured continuously through time or estimated as changes during the interval between discrete time measurements; these variables are often rate functions and reflect system dynamics.

Table 6.1 is a classification of structural and functional variables which have been identified. "Individual" refers to individual organisms and "population" is the intraspecific population group. "Community" can be defined as all the living organisms of an area or as interspecific groups of organisms with similar life modes or habitat preferences (e.g., benthic invertebrates, zooplankton, phytoplankton, macrophytes), equivalent to Odum's (1971) minor communities. The "watershed" level refers to the entire set of living organisms and biological processes in a body of freshwater as influenced by external loading. It is implicitly recognized that environmental coupling occurs at each level of biological organization. Measurable variables may overlap between levels of organisms as is evident from the table. In addition,

Table 6.1. Measurable structural and functional biotic variables at different levels of hierarchical organization used or of potential use in impact analysis.*

Individual	Population	Community	Watershed
Structural:			
Presence/Absence	Density No. Individuals Biomass	No. Individuals	CPOM/FPOM
Mass		No. Species	Detrital C/N
Morphology	Distribution	Key Species	Dominant Functional Groups
Histopathology	Size/Age Structure	Diversity Richness Evenness	Food Chain Structure
Chemical Composition Elements Compounds	Chemical Composition Elements Compounds		Total Organic Matter
		Biomass	Inorganic Nutrients
		Chemical Composition Elements Compounds	Biochemical Diversity
			Pattern Diversity
Functional:			
Energetics Ingestion Egestion Assimilation Respiration Production	Energetics Ingestion Egestion Assimilation Respiration Production	Gross/Net Production	Gross/Net Production
		Community Respiration	Total Respiration
		P/R	P/R
		P/B	P/B
Tolerance Living/Dead	Biotic Potential Natality Mortality	Biochemical Activity	Material Flux/Cycling
Behavior	Dispersal Drift Invasion Avoidance		Trophic State Oligotrophic Mesotrophic Eutrophic Dystrophic
No. Offspring			
Biochemical Activity	Tolerance LC_{50}		Trophic Type Autotrophic Heterotrophic
	Biochemical Activity		Stability

*See text for definition of terms.

some variables such as trophic state have structural and functional aspects, although they have been listed under functional variables.

In general, the ensuing discussion follows the format of Table 6.1, considering first the structural properties of organisms and populations, community components, and watershed ecosystems, and then the functional properties of those organizational levels. In some instances more than one level of organization is considered under a particular topic. Also, in some cases variables are considered in the context of a particular approach to investigation. These deviations from the organizational scheme are mainly for the convenience of discussing related ideas.

6.2 STRUCTURAL BIOTIC VARIABLES

6.2.1 Individual and Population Level

Despite Forbes' (1887) early recognition of the importance of functional relationships in aquatic ecosystems, the first approaches to impact assessment dealt primarily with structural properties of organisms, populations, and communities. The saprobien system of Kolkwitz and Marsson (1908, 1909) is a classification system based on their observation that certain organisms are commonly associated with a series of saprobic zones of decreasingly severe environmental conditions downstream from organic waste discharges. Lists of species associations are used to define these zones according to the presence or absence of tolerant indicator organisms. Various modifications of this scheme have been used to evaluate the effects of pollution on aquatic life, particularly microorganisms and benthic macroinvertebrates (Richardson 1921, 1928; Hentschel 1925; Whippel 1927; Naumann 1932; Campbell 1939; Butcher 1947; Wuhrmann 1951; Gaufin and Tarzwell 1952; Beck 1955). Rigid application of the indicator organisms concept in pollution studies has received criticism for several reasons: 1) tolerant organisms exist in other than polluted environments, 2) environmental factors other than pollution limit the distribution of species, 3) classification of organisms into tolerant, facultative, and intolerant categories is subjective since tolerances vary under different environmental conditions, 4) considerable time and taxonomic skill is required on the part of investigators and decision makers, and 5) the indicator organism concept was developed for degradable organic wastes and may be inappropriate for toxic or growth-stimulating pollutants (Cairns, Dickson, and Lanza 1973; Patrick 1973; Brinkhurst 1974; Hellawell 1977; Turoboyski 1977).

Recognition of these shortcomings led to the development of assessment techniques which consider alterations in aquatic community structure caused by perturbations, mostly organic and toxic waste discharges. In this approach, the relative abundance of species in a community is considered to be a more reliable indicator of environmental stress than the mere presence or absence of indicator species (Gaufin 1973).

One of the earliest approaches to aquatic structural analysis was developed by Patrick (1949). In her studies of algae she noted that undisturbed streams frequently contain large numbers of species (many diatoms) with none in great abundance. She found that organic pollution reduced the number of species, caused unevenness in population sizes, and often resulted in a shift to filamentous green or blue-green algal dominance. Her impact assessment scheme classified algae into seven groups on the assumption that those within a group respond similarly to stress. Frequency distributions of numbers of species and individuals within groups at polluted versus unpolluted sampling sites are used to assess the severity of impact. A modified version of Patrick's method (in a saprobien system context) was used to assess the impact of organic wastes on stream macroinvertebrates (Wurtz 1955). Four life mode categories (pelagic, sessile, foraging, and burrowing), were employed and pollution tolerant and intolerant species within these groups were rated.

An analysis by Gaufin and Tarzwell (1956) demonstrated the quantifiable nature of structural changes in stream macroinvertebrate and microorganism communities affected by sewage discharges. They too found relatively small numbers of species but large numbers of individuals in stressed environments.

The "Catherwood Diatometer," based on the observation that species-abundance relationships frequently display log-normal distributions, was used by Patrick et al. (1954) for analyzing algal community structure. Diatom communities developing on artificial substrate sampling devices showed typical log-normal modal distributions in undisturbed environments. Moderate organic pollution caused shifts in the modal curve peak while heavy pollution depressed the curve. Toxic pollution resulted in reduced height and width of the modal curve (Patrick 1973).

6.2.2 Community Level

Assessments of the structural response of entire biotic communities (i.e., all community components combined) to environmental perturbations in aquatic systems have not been numerous. Undoubtedly this is partly due to time and expense constraints. But more importantly, meaningful interpretation of large quantities of biotic and abiotic information has had to await an ecosystem perspective toward impact assessment. The interdependencies which exist among community components can be described in terms of the transmission of perturbations through causal networks in aquatic systems (Patten 1973) and thus, an impact in one component, can have repercussions in others apparently far removed in space or time. A number of the saprobien system approaches have attempted to describe overall biotic community structure in flowing waters by considering presence, abundance, and tolerance information from nearly all groups present in a study area (e.g., phytoplankton, zooplankton, periphyton, bacteria, fungi, benthic invertebrates, fish)(Hawkes 1977). The pollution studies by Gaufin and Tarzwell (1952) included several community components (bacteria, blue-green algae, flagellates, and protozoa), but the major emphasis was on structure of the macroinvertebrate component. Few investigators have defined relationships among all components. The approach used by Cummins (1975) integrates a number of biotic and abiotic components and processes in stream ecosystems and is discussed in the next section.

One of the earliest total ecosystem investigations was conducted in the Savannah River to assess the impact of a nuclear power plant discharge on biotic community structure (Patrick et al. 1967). The structure of the whole community of species of all major groups of organisms, the relation between groups, and the physical and chemical properties of the river were studied. Some findings were: 1) numbers of species in the various communities showed little seasonal or year-to-year change; 2) significant variations in kinds of species occurred seasonally and yearly, many species appearing only once and a few occurring at all sampling stations or on all sampling dates; 3) significant overlap of species occurred between sampling stations on a particular sampling date, the degree of overlap being greatest for fish and diatoms (this was attributed to mobility of fish and rapid population growth of diatoms in response to changing environmental conditions; 4) some algal and insect species showed seasonal trends in abundance; 5) the occurrence of some species was correlated with ambient temperature, turbidity, alkalinity, iron and magnesium levels, and certain fish and diatom occurrences were associated with river flow conditions; 6) no distinct species associations were evident, but representatives from the fish, insect, protozoa, and diatom communities were always found together. From observations it was concluded "that the transient environment is more important in determining the occurrences of most of the species encountered than the permanent physical environment." Stable water levels created by the Clark Hill Dam increased the stability of riverbank habitats and decreased water turbidity, resulting in greater algal production and food availability.

A number of biotic and abiotic variables were studied in three Michigan streams receiving different levels of nutrient enrichment (Ball et al. 1973). The objectives were "to develop indices for predicting changes in streams as they are subjected to increasing eutrophication, to obtain baseline data that relate stream characteristics to water quality, to evaluate the effects of urbanization on stream stability, and to measure the aesthetic and recreational values of the streams." Investigations were conducted on aquatic macrophytes, periphyton, benthic macroinvertebrates, and fish communities in addition to several chemical and physical factors. It was found that: 1) variance in stream discharge and amount and variability of macroinvertebrate drift were related to the degree of human disturbance in the watersheds; 2) macroinvertebrate species and genus diversity were positively correlated with water quality; 3) periphyton species and genus diversity (from artificial substrates, were negatively correlated with water quality, although certain diatom groups showed positive trends; 4) variance in macrophyte standing crop was positively correlated with stream nutrient loading; 5) macrophyte tissue phosphorus content was related to concentrations of phosphorus in the water, the plants probably being phosphorus-limited (tissue nitrogen content was related to tissue phosphorus but independent of nitrogen concentrations in the water; and 6) trout were less abundant, but individuals were larger in eutrophic streams.

The dependence of phytoplankton community structure on the nature of higher trophic level communities and abiotic variables was demonstrated by Shapiro et al. (1975) in several Minnesota lakes. Using large polyethylene bag enclosures in situ, they showed that: 1) the presence of zooplanktivorous fish (perch) caused a significant increase in algal abundance due to the demise of the herbivorous zooplankton community; 2) the presence of bottom feeding fish (carp) resulted in increased chlorophyll levels because of nutrient regenerating activities of the fish (i.e., bottom feeding fish act as "nutrient pumps"); and 3) lowering of ambient pH levels (with CO_2 or HCl) caused the phytoplankton to shift from blue-green- to green-algal dominance, most likely due to the competative advantage green algae have in the presence of available CO_2 (additions of Cl_2 caused the same change in community structure, possibly because blue-green algae became stressed and more susceptible to cyanophages). Selective grazing by zooplankton can significantly alter phytoplankton community structure (Sorokin 1968; Porter 1972, 1973, 1975). Certain blue-green algae are apparently unaffected by passage through the guts of zooplankton and may even be provided with nutrients during the process; as a result such forms may increase in relative abundance among the phytoplankton.

Biotic Indices

The length of time required to properly collect and analyze species-abundance data and difficulties of interpretation, led to the development of techniques which convert community structure information into numeric indices. Index scales often are divided into segments associated with relative degrees of stress and thus are more easily managed and interpreted by non-biologists. A phytoplankton quotient index has been used to assess nutrient enrichment of lakes (Nygaard 1949). This compound index, developed by Patrick (1973), is based on numbers of species of various taxonomic groups of algae present at sampling sites and is given by:

$$\frac{\text{Myxophyceae} + \text{Chlorococcales} + \text{Centrales} + \text{Euglenineae}}{\text{Desmidieae}}$$

Values less than 1 are found in nutrient poor lakes while values greater than 1 indicate increasing degrees of nutrient enrichment. A form of Nygaard's index was used in studies of nutrient enrichment of Lake Washington (Stockner and Benson 1967). However, these indices are highly variable even within a particular lake district (Wetzel 1975).

A pollution index was derived from the saprobien system by assigning numeric values to saprobic zones and enumerating the occurrence of species characteristic of particular zones (Pantle and Buck 1955). The index, S, is given by

$$S = \frac{\Sigma rh}{\Sigma h}$$

where r = saprobic zone rating, and h = occurrence rating. A "biotic index" based on the abundance of intolerant (Class I) and tolerant (Class II) species of macroinvertebrates was developed by Beck (1955) for assessing the impact of organic pollution on streams;

$$\text{Biotic Index} = 2(n\ \text{Class I}) + (n\ \text{Class II})$$

where n = number of species in the appropriate class. Values less than 1 imply severe impact, 1 to 6 moderate impact, and 6 to 10 little or no impact. A bivariate statistical technique was used to assess the response of four taxonomic groups of benthic macroinvertebrates to industrial wastes in a large lake (Beak et al. 1959). Abundance of organisms in samples collected along concentric transects away from the outfall was plotted on statistical control charts. The method proved sensitive to toxic pollution.

Diatom community structure was incorporated into an index of organic pollution impact by Wantanabe (1962). Occurrence data for intolerant (A), indifferent (B), and tolerant (C) species are used in the formula

$$\frac{2A + B - 2C}{A + B + C} \times 100$$

to calculate the index. This system was modified to account for varying degrees of tolerance among the groups and to describe communities characteristic of saprobic zones similar to those in the saprobien system (Fjerdingstad 1964).

Palmer (1969) proposed an algal pollution index based on a consensus of algal tolerance ratings derived from the literature. The index is the sum of tolerance scores for all algal species or genera present in a water sample.

The major problem inherent in most of these impact assessment schemes is their reliance on species tolerance ratings which have for the most part been subjective rather than empirically based (Gaufin 1973). Cairns (1977), however, feels that "a sufficiently large information base" on species tolerances is foreseeable and that the saprobien system approach could become useful. In fact, Resh and Unzicker (1975) point out that the indicator organism/saprobien system concepts have been "accepted and applied" in most of Europe and the Soviet Union but not in Great Britain or North America.

The indexing systems most commonly used in Europe and the ecological information used in their formulation have been discussed by Hawkes (1977) (Tables 6.2 and 6.3). The Trent Biotic Index (Woodiwiss 1964) incorporates the presence or absence of indicator organisms and reduction in numbers of species of macroinvertebrates to produce a numeric score. A rating scale from 0 to 10 distinguishes degrees of disturbance from severe to slight. The Chandler Biotic Index (Chandler 1970) is based on macroinvertebrate indicator organisms, numbers of species, and numbers of individuals, and is supposedly more sensitive to mild organic pollution than the Trent Index (Hawkes 1977; Solbe 1977). Cook (1976) compared the Chandler Index to the Shannon-Weaver diversity index and found it more reliable in assessing changes in macroinvertebrate community structure. Variations of the saprobien system, in addition to those mentioned above, (e.g., Zelinka and Marvan 1961; Sladecek 1969; Peschek 1974), are used in Germany, Poland, Austria, Hungary, Yugoslavia, Denmark, Bulgaria, and Czechoslovakia (Alabaster 1977; Turoboyski 1977) for assessing the impact of pollution on surface waters. These schemes often include information concerning indicator organisms and species abundance of nearly all taxonomic groups present at a sampling site (bacteria, fungi, protozoa, algae, invertebrates, etc.). In Spain diversity indices (Margalef 1951, 1957) are used in impact assessment (see below).

Table 6.2. Some classifications of river water quality zones. (From Hawkes 1977.)

Zones	Information most utilized Response*	Taxa
Germany		
Polysaprobic, α-mesosaprobic, β-mesosaprobic, oligosaprobic (Kolkwitz and Marsson 1908, 1909)	A	All
W. Germany		
Classes 0-5 (Besch 1973)	A	All
United States		
Septic, contaminated, recovery, clean (Richardson 1928)	A	Invertebrates
Five biological zones (Brinley 1942)	A	Planktonic-microorganisms
Septic, recovery, clean (Wurtz 1955)	A, D	Benthic invertebrates
Septic, recovery, clean water (Gaufin and Tarzwell 1952)	A	Benthic invertebrates
Switzerland		
K-M system with α-, β- and γ-polysaprobic zones (Thomas 1944)	A	All
10 zones according to autotrophy-heterotrophy (Wuhrmann 1951)	A, E	Benthic microorganisms
England		
Foul pollution, pollution, mild pollution, repurified water (Butcher 1946)	A	Benthic invertebrates and algae
Gross organic pollution (P), macrofauna restricted (αM)		All
Pollutional forms dominant (βM)		All
Indications of slight organic pollution (o-βM), good quality (O)		

Table 6.2 (Continued).

Zones	Information Most Utilized Response*	Taxa
England (continued)		
Toxic--all life restricted (Hawkes 1956)	A, C	
England and Wales		
Classes A-B-C-D (Department of Environment 1972)	A	Benthic invertebrates and fish
Czechoslovakia		
Antisaprobic, hypersaprobic-a + b, polysaprobic-a + b	A	All
Mesosaprobic, oligosaprobic, katharobic (Sramek-Husek 1956)		
Denmark		
Coprozoic, polysaprobic, mesosaprobic, oligosaprobic	A	Benthic phyto-microorganisms

*Biocoenotic responses of indicator value induced by polluting discharges

A - Appearance or disappearance of individual species of indicator value
B - Reduction in numbers of species or taxa
C - Changes in the populations of individual species
D - Changes in the proportional species composition of the community
E - Changes in the degree of heterotrophy-autotrophy
F - Changes in the degree of productivity

Table 6.3. Some biological indices used in river water quality classification. (From Hawkes 1977.)

Index	Information Most Used Response*	 Taxa
Czechoslovakia		
Biological Index (I) based on proportion of producers-consumers-decomposers (Gabriel 1946)	E	Plankton
Zelinka and Marvan 1961	A, C	All
Sladecek 1969	A, C	All
United States		
Biotic Index 0-40 (Beck 1955)	A	Invertebrates
Palmer Index (Palmer 1969)	A, B	Algae
England		
Trent Biotic Index 0-10 (Woodiwiss 1964)	A, B	Invertebrates
Scotland		
Simplified Trent Biotic Index 6-1 (Lothian River Purification Board 1955)	A, B	Invertebrates
Score system 0-infinity (Chandler 1970)	A, B, C	Invertebrates
France		
Modified Trent Biotic Index to take account of river zonation (Tuffery and Verneaux 1968)	A, B	Invertebrates
Germany		
Based on Saprobic System. Using a saprobity value and the relative abundance of each species present, the saprobic classification of the zone is calculated (Pantle and Buck 1955; Knopp 1954)	A, C	All

Table 6.3 (Continued).

Index	Information Most Used Response*	 Taxa
Spain		
Diversity Index (Margalef 1951)	B, C	
Diversity Index (Shannon and Weaver 1949; Wilhm and Dorris 1968)	B, C, D	

*Biocoenotic responses of indicator value induced by polluting discharges

A - Appearance or disappearance of individual species of indicator value

B - Reduction in numbers of species or taxa

C - Changes in the populations of individual species

D - Changes in the proportional species composition of the community

E - Changes in the degree of heterotrophy-autotrophy

F - Changes in the degree of productivity

Several criticisms have been levied against these indexing systems. Biotic indices, even though numeric values, are not amenable to statistical analysis and result in a loss of information which might add significantly to data interpretation (Hawkes 1977). Saprobien system indices were originally developed to assess the effects of degradable organic pollution on aquatic systems. The changed nature of pollution in recent years (i.e., the presence of toxic substances and nutrients) renders such indices inappropriate (Patrick 1973; Turoboyski 1977). Also, they require species tolerance information which is often lacking (Gaufin 1973).

Diversity Indices

In the last two decades species diversity indices have received considerable attention, particularly in North America, as potential tools for assessing the impact of environmental disturbances on aquatic community structure. A number of indices have been proposed, and Pielou (1969) and Peet (1975) discussed the formulation and ecological applicability of most. Three distinct types of diversity indices are generally recognized (Peet 1974): 1) richness, based on importance or numbers of taxa; 2) equitability, based on the evenness with which importance is distributed among the taxa; and 3) heterogeneity, based on richness and equitability. Some of the earlier biotic indices were similar to the first and second type, while recent impact assessment studies have used the latter type.

Margalef (1951, 1957) and Patten (1962) first proposed the use of diversity indices derived from information theory (Shannon and Weaver 1949) to describe the structure of natural phytoplankton communities. Since then the Shannon-Weaver index has been widely used in assessing the impact of pollution on aquatic community structure (e.g., Wilhm and Dorris 1966, 1968; Mathis and Doris 1968; Wilhm 1968, 1970; Staub et al. 1970; Nuttall and Purves 1974; Devaux 1975; Nauman and Kernodle 1975; Chisholm and Downs 1977; Clarke 1977; Hakkari and Gramberg 1977; Solbe 1977). The United States Environmental Protection Agency (Weber 1973c) has recommended use of the Shannon-Weaver diversity index and Lloyd and Ghelardi's (1964) equitability index for analyzing aquatic macroinvertebrate community structure in water quality surveys. It frequently has been observed that species diversity is lower in polluted than in nonpolluted environments due to disappearance of sensitive species and increase in abundance of insensitive species. The expected values for Shannon-Weaver diversity are: heavily polluted 0 - 1; moderately polluted 1 - 3; unpolluted greater than 3 (Wilhm 1972).

A number of investigators have recently questioned the ecological validity of diversity indices on mathematical, theoretical, and practical grounds; others have criticized the indiscriminate use of the indices in impact analyses, especially to the exclusion of direct considerations of species-abundance data (Archibald 1972; Hamilton 1975; Odum 1975; Peet 1975; Winner et al. 1975; Harrell and Duplechin 1976; Stoneburner et al. 1976; Zand 1976; Hawkes 1977; Godfrey 1978). Indeed, Hurlbert (1971) has suggested that the concept be completely abandoned in favor of direct evaluations of species-abundance data. Hawkes (1977) suggested that diversity indices are most appropriate in studies of the impact of toxic substances and physical perturbations which "impose stress generally." In terms of impact assessment, diversity indices appear to be useful when considered with other types of species-abundance data analysis, but are of limited value as sole indicators of biotic response.

A major limitation to the use of biotic and diversity indices arises from taxonomic difficulties. Specific identification of aquatic organisms is often difficult, if not impossible, with the result that genera and even families are used in the calculation of indices. The wide range of organismal tolerances, even within a particular genus, renders such calculations of questionable value (C. I. Weber, personal communication). K. W. Cummins (personal communication) suggests that mathematical expressions which indicate redundancy in a system frequently indicate redundancy in the taxonomy. He feels that the widespread use of biotic indices in Europe may be the result of a simpler and better developed taxonomy (at least for invertebrate fauna).

Multivariate Statistical Approaches

In recent years, multivariate statistical techniques have been used to analyze benthic community structure, taking into consideration numerous biotic and abiotic variables (Brinkhurst 1974). Bivariate control charts used by Beak et al. (1959) represent one of the earliest analytical tools. Cluster analysis has been used to group sampling stations according to their biotic similarity (Huges and Thomas 1971; Kaesler and Cairns 1972). Factor analysis has been used to distinguish among macroinvertebrate communities based on such variables as water depth, substrate texture, and species composition (Lie and Kelly 1970; Clarke 1977). Cassie and Michael (1968) employed multiple regression and principal component analysis to show the response of benthic communities to sediment particle size and organic content. These techniques are best applied to data from small areas which have been intensively sampled (Brinkhurst 1974). However, multivariate analysis of data from large areas might provide insight into regional patterns of community structure.

Keystone Species

It is obvious from the above discussion that qualitative and quantitative considerations of the presence/absence, abundance, and distribution of individual organisms and taxonomic groups (particularly invertebrates and algae) have been major themes in aquatic environmental impact analysis. An important concept which has apparently escaped the attention of investigators is that of the "keystone species" (Paine 1966, 1969). In his studies of an intertidal marine community, Paine showed that exclusion of the starfish *Pisaster* resulted in proliferation of mussels (*Mytilus*) and barnacles (*Mitella*) normally held in check by starfish predation. This, in turn, caused displacement of several other species and the community was reduced from fifteen to eight species. Although not dominant in numbers, biomass, or energy flow through the community, *Pisaster* exerted a commanding influence on community structure and was thus designated the "keystone species" in the community. Similar phenomena have been observed by other investigators (McLean 1962; North 1965; Mann and Breen 1972; Brinkhurst 1974).

The keystone species concept was elaborated into one of "action categories of key species" which exert a "disproportionate influence on the kinds of plants and animals that live together." The following action categories are quoted directly from Brinkhurst (1974, p. 77):

> 1. Species that add to the physical structure of the habitat such as dominant plant species and coral. Decreased heterogeneity in physical structure due to removal of one of these species could eliminate several others that require the structure for refuge or attachment.
>
> 2. Some species alter or disturb the substrate surface by digging or burrowing, such as do carp or tube-dwelling polychaetes. The activities of one such species can greatly alter faunal composition.
>
> 3. Species that occupy the substrate in a contiguous manner and by their presence physically force out many other species. Intertidal mussels and barnacles fit into this category.
>
> 4. Single herbivore species that have the capacity to decimate stands of vegetation.
>
> 5. Carnivores that act to prevent domination of the community by species in categories 2 to 4.

The best way to identify keystone species and their influence on a community may be through field enclosure experiments in which habitats or species assemblages are altered (Brinkhurst 1974). Techniques for such an analysis are not yet well developed, especially for stream ecosystems (K. W. Cummins, personal communication). However, if such species or action categories could be identified in impact assessment studies, they might be designated with a "red flag" (Odum and Cooley 1976) along with endangered and commercially important species. The concept deserves further research.

Analytical Chemistry Approach

Another approach to the study of biotic structure in response to environmental perturbations has been from a molecular perspective. Pollution studies often have been concerned with specific chemicals and thus the importance of measuring the chemical composition of aquatic organisms has been recognized. The phenomenon of biological (food chain) magnification of elements and compounds in ecosystems has been documented well (Woodwell 1970), especially for fat soluble pesticides (Odum et al. 1969; Canton et al. 1975), radionuclides (Foster and Rostenbach 1954; Aberg and Hungate 1967; Nelson and Evans 1969), and heavy metals (D'Itri 1971; Duce et al. 1972; Andelman 1973). Chemical and histopathological analysis of tissues from organisms or populations at various trophic levels provide a means of assessing the impact of specific substances on the entire biotic community. Higher trophic levels are of particular interest since this is where signs of stress often first appear. Fish (Bligh 1970) and crayfish (Armstrong and Hamilton 1973) have been suggested as indicators of mercury contamination in freshwaters.

The elemental composition of aquatic algae and macrophytes has been proposed as a measure of the nutrient status of aquatic ecosystems. High phosphorus concentrations in the surrounding medium result in luxury consumption of phosphorus by algae (Fitzgerald and Nelson 1966). Luxury consumption of nitrogen and phosphorus by aquatic macrophytes was found under various nutrient regimes in laboratory experiments (Gerloff and Krombholz 1966). "Critical levels" of tissue element concentration (i.e., levels associated with maximum growth rate) were determined for several species and compared with the elemental content of plants collected from natural lakes. Nutrient limitation in the lakes was indicated by tissue concentrations below the critical level. Interspecific and seasonal differences in tissue nutrient content were found. The use of *Elodea occidentalis* in bioassays of nutrient availability in freshwaters has been suggested since critical levels of nutrients have been determined (Gerloff and Fishbeck 1973).

The importance of nutrient ratios (e.g., C:P, N:P, Si:P) has been determined from studies of nutrient limitation in aquatic systems (Fuhs et al. 1972; Kramer et al. 1972; Rhee 1978). A nutrient may be limiting if its concentration ratio in natural waters does not bracket the composition of the organism and that "organism composition requires information on nutrients in the water as well as other environmental parameters" (e.g., light and temperature)(Kramer et al. 1972).

Margalef (1975) proposed a ratio

$$\frac{\text{Amount of the element in the environment}}{\text{Amount of the element in the organisms}}$$

for any essential element, as a measure of the trophic state of aquatic ecosystems. He reasoned that in eutrophic systems "every atom spends, on the average, more time outside the living organism" resulting in a higher value for the ratio than in oligotrophic systems. He also suggested that the phytoplankton biomass/zooplankton biomass ratio is higher in eutrophic than in oligotrophic lakes.

The biochemical composition of organisms, populations, and communities has been shown to respond to environmental perturbations. Total living organic matter or biomass is frequently used as a measure of biotic state (American Public Health Association 1976) and species biomass data can be incorporated as importance values into diversity indices (Whittaker 1975). Direct measurement of living biomass in natural systems (e.g., gravimetric determinations or total organic carbon analyses) is often confounded by the presence of non-living organic matter and therefore several corollary approaches have been proposed.

Holm-Hansen et al. (1968) suggested that nucleic acid concentrations in water samples might be indicative of living biomass. Subsequent work, however, has shown the existence of wide seasonal and interspecific variations in nucleic acid concentrations (Baudouin and Scoppa 1975) and relatively long molecular survival times following cell death (Holm-Hansen 1969).

Adenosine triphosphate (ATP) concentrations in seawater have been used as a measure of viable microbial biomass and abundance (Holm-Hansen 1969).

This technique has been widely used in aquatic research at individual, population, and community levels of organization (Holm-Hansen 1969; Patterson et al. 1970; Lee et al. 1971; Brezonik and Patterson 1972; Rudd and Hamilton 1973; Weber 1973; Champait and Larpent 1978). Standard analysis procedures are described in Strickland and Parsons (1968) and American Public Health Association (1976). ATP levels in bacteria and algae respond rapidly to heavy metals and nutrient limitations (Holm-Hansen 1970; Brezonik et al. 1975). However, significant seasonal and intra- and interspecific variations may exist in ATP concentrations rendering the method unreliable as a measure of biomass in natural communities (Bott 1973; Skjoldal and Barenstedt 1977; Ivanovici 1977).

Photosynthetic plant pigments have long been used to assess the state and abundance of phytoplankton and periphyton in natural and experimental aquatic systems, and numerous analytical techniques have been described (Manning and Juday 1941; Richards and Thompson 1952; Edmundson and Anderson 1956; Steeman-Nielsen 1962; Parsons and Strickland 1963; Ricketts 1967; Yentsch 1967; Strickland and Parsons 1968; Ganf 1974; American Public Health Association 1976).

The relative abundance of various photosynthetic pigments in a mixed algal community is reported to indicate the taxonomic composition of the community (Round 1965; Wetzel 1975). Margalef (1968) suggested that pigment diversity is a good measure of the physiological state of planktonic communities and proposed the pigment index

$$\frac{D_{430}}{D_{665}}$$

where acetone extract absorbances are measured at 430 nm (carotenoid pigments) and at 665 nm (chlorophyll $\underline{a}$). During community succession the pigment index increases, reaching highest values as the community ages (yellow pigments predominating). Values ranging from less than 2.5 in freshwater lakes dominated by green algae, to greater than 8 in older communities dominated by dinoflagellates have been reported (Margalef 1968).

The applicability of an autotrophic index (AI) to impact assessment of organic pollution has been considered by Weber (1973a). From the equation

$$\mathrm{AI} = \frac{\text{Biomass (dry weight organic matter)}}{\text{Chlorophyll } \underline{a}}$$

the trophic nature (autotrophic versus heterotrophic) of aquatic communities can be determined; as heterotrophy increases, values of the index increase. Values from 50 to 100 have been reported for natural communities in undisturbed environments with values as high as 1000 downstream from sewage discharges. The ratio, ATP/chlorophyll $\underline{a}$, has been suggested as a measure of trophic state (Brezonik et al. 1975). The ratio of chlorophyll a to phaeophytin a (a degraded form of chlorophyll a) is useful in assessing the physiological state of algal communities (Weber 1973a).

6.2.3 Watershed Level

Integration of the responses of all biotic and abiotic components to environmental perturbations in a lake or stream transforms the problem of impact assessment to the ecosystem level of organization. In practice, of course, it is not possible to measure all variables in an ecosystem. Alternatively, certain key variables can be studied which integrate or reflect the behavior of all ecosystem components.

Cummins (1975) proposed a set of parameters for assessing "key community functions of running water ecosystems." Four ratios from his list reflect the structural order of stream ecosystems but in practice are considered along with several functional variables discussed in the next section:

1. Coarse particulate organic matter/fine particulate organic matter, (CPOM/FPOM), measured as ash-free dry weight of bottom and drift samples, decreases from 0.25 - 0.50 in headwaters to lower values as stream order increases.

2. Carbon/Nitrogen, measured as elemental C/N in detritus from sediment and in transport, decreases as microbial colonization of detritus particles increases.

The following two parameters incorporate what Cummins has called "dominant functional groups" in stream ecosystems (freshwater invertebrates grouped according to feeding characteristics). Shredders and collectors are detritivores which feed on microbially colonized CPOM and FPOM, respectively; grazers feed on photosynthetic tissue of algae and vascular macrophytes. From these classifications Cummins formulated two parameters.

3. Shredders/Collectors, measured as animal biomass from leaf packs and CPOM/FPOM samples, has highest values in headwaters when "leaf pack processing is greatest and $P/R < 1$."

4. Grazers/Detritivores (i.e., shredders and collectors), measured as animal biomass from bottom sediment and leaf pack samples, has highest values when $P/R > 1$.

While these parameters were derived from studies of small streams, they should be applicable to higher order streams as well (Cummins 1975). He states that "once the ranges for the parameters have been determined along non-perturbed river systems (or portions of systems) in different geographical regions..., deviations from generalized theory should be readily discernible and the particular community functions affected identified."

Odum (1969) listed 24 "ecosystem attributes" and their trends expected during ecological succession. From that list the following may be defined as structural properties: food chain length and configuration, total organic matter, inorganic nutrients, species diversity, biochemical diversity, stratification, and spatial heterogeneity. Woodwell (1970) and Margalef (1975) have suggested that the response of an ecosystem to environmental perturbations (especially nutrient enrichment) may be a digression to an earlier successional state. If this and the successional trends predicted by Odum (1969) are true, then these variables should be important considerations in impact assessment.

6.3 FUNCTIONAL BIOTIC VARIABLES

Broadly, functional biotic variables may be defined as those which reflect the dynamics of living systems and which relate to energy/matter processing at any level of biological organization. Environmental impact analysis studies have been concerned with several types of functional variables which may be considered as special cases of the above definition:

1. Physiological and biochemical activity (gaseous exchange, nutrient uptake, excretion, enzyme activity, etc.) have been used as indicators of stress in macroorganisms and populations of microorganisms. More recent studies have focused on biochemical activity (e.g., adenylate energy charge) of natural communities in perturbed and unperturbed environments.

2. Behavior (especially movement, such as taxis, trophism, migration, feeding activity) is essentially an organismal phenomenon but has higher level manifestations in the organization and maintenance of populations and communities (e.g., symbiotic relationships)(Odum 1971). Avoidance responses of motile organisms to unfavorable environmental conditions are behavioral activities of particular relevance to impact analysis.

3. Reproductive patterns (natality, mortality, biotic potential, fecundity, dispersal) occur at the population level of organization and are often sensitive to environmental disturbances.

4. Bioenergetics refers to functional biotic properties associated with the flow of energy or matter through living systems. Bioenergetic budgets for organisms and populations are based on rates of ingestion, egestion, assimilation, respiration, and production (including growth and yield), most of which have been used as response variables in perturbation studies.

These processes have been described at organism, population, and community levels of organization and form the basis for ecosystem trophic models. While these four categories are not exhaustive of biological functions, they are representative of the variables most applicable to environmental impact analysis.

In general, functional biotic variables have not been studied as extensively in aquatic systems as their structural counterparts perhaps because methodologies have been a relatively recent development. In addition, some are based on theoretical and even controversial concepts making them more of heuristic than of practical utility. Nonetheless, any meaningful evaluation of the effects of human activity on freshwater ecosystems must consider the processes which underlie biotic structure. Many of these processes are current themes in limnological research and are finding applications in environmental stress studies.

6.3.1 Individual and Population Level

Functional biotic variables have most often been studies at the organism and population levels of organization in laboratory investigations. Bioassays have been widely used in impact assessment and have incorporated a number of functional response variables. Extensive literature reviews and aquatic bioassay methodologies are presented in Cairns and Dickson (1973), Glass (1973), Weber (1973c), Lesel (1976), and American Public Health Association (1976). Two types of bioassays are recognized: 1) in situ bioassays in which organisms are caged or contained in an environment under study; and 2) laboratory bioassays in which organisms are exposed to substances or conditions in controlled laboratory experiments (Weber 1973c). The latter type may be static or flow-through and of short, intermediate, or long-term duration (American Public Health Association 1976).

Most bioassay studies concerned with impacts in aquatic systems have been static, short-term laboratory tests conducted on freshwater fish. The response variable is usually death of the test organism and the objective is determination of the concentration of toxicant lethal to 50 percent of the test population (LC_{50}). These experiments are still widely used, but the scope of bioassay methodology has been broadened to include a variety of taxonomic groups, long-term duration to cover life cycles of test organisms, and a number of additional functional variables. Table 6.4 is a partial summary of taxonomic groups and response variables used in long-term (life cycle) bioassays (American Public Health Association 1976). Several of the methods described are for marine organisms, but the basic methodology and variables should be appropriate for the respective freshwater counterparts. In addition to the response variables listed for fish, opercular movement, locomotion, and feeding activity are useful measures in bioassays (Weber 1973b).

Biostimulation or nutrient limitation bioassays have been used to assess the response of algae to nutrient enrichment and to determine the availability of nutrients to algae in natural waters (Goldman 1962, 1965, 1969; Fitzgerald 1969, 1972; Allen 1972; Fuhs et al. 1972; Maloney et al. 1972; Powers et al. 1972; Jones and Bachman 1975; Maslin and Boles 1978). Some of these studies have examined natural phytoplankton communities in situ, some have been conducted in laboratories on unialgal cultures, and a number of response variables have been measured in both cases (e.g., productivity, growth rate, chlorophyll a). Suggested standard procedures for unialgal biostimulation assays are given in Vollenweider (1969a), Environmental Protection Agency (EPA)(1971), Weber (1973c) and American Public Health Association (1976). The algal assay procedure bottle test (EPA 1971) was used to evaluate the nutrient

Table 6.4. Organisms and response variables used in long-term (life cycle) bioassays. (Summarized from American Public Health Administration 1976.)

Taxonomic Group	Response Variables
1. Phytoplankton	Maximum specific growth rate
2. Zooplankton	
Protozoa	Population growth rate; population density; accumulation of residues
Daphnia	Reproductive impairment
3. Coral (marine)	Morphological changes; mucus production feeding rate; cilliary currents; calcification
4. Polychaetes (marine)	Larval survival and development; egg production
5. Crustaceans	
Amphipods	Growth; reproductive success; survival of offspring
Crayfish	Survival of offspring
Crabs (marine)	Egg hatchability; larval survival and development
Lobsters (marine)	Egg hatchability; larval survival and development
Shrimp	Egg hatchability; larval survival and development
6. Insects	Reproduction; growth; emergence; metabolism
7. Molluscs (marine)	Reproduction; growth (shell deposition); byssal thread secretion; morphological change; larval development; residue accumulation
8. Fish	Morphological, physiological, biochemical change; egg viability and hatchability; larval growth and survival; residue accumulation

status of 44 lakes and streams in North Carolina (Weiss 1976). It was concluded that analysis of N:P ratio in the original water sample provides the same information as derived from the more complicated assay spiking procedure if no other factors are growth limiting.

Four types of algal assays have been recognized: 1) ^{14}C bioassays; 2) continuous culture enrichment studies; 3) in situ enrichment studies in enclosures; and 4) whole lake enrichment studies (Gerhart and Likens 1975). An evaluation of the first three types in a New Hampshire lake showed that the short term, in situ ^{14}C bioassay (recommended in Vollenweider 1969a) gave results inconsistent with the others. It was concluded that information derived from this test may not be relevant to the problem of eutrophication or even to the growth of phytoplankton in nature, and that the standard procedures should be re-evaluated (Gerhart and Likens 1975). Maslin and Boles (1978) pointed out that all nutrient-enrichment bioassays are subject to significant alteration of the chemical nature of the sample but argued that this is in fact the purpose of such tests. They proposed a multiple nutrient enrichment bioassay for determining algal nutrient limitations in natural waters.

The algal assay procedure bottle test (EPA 1971) was compared with a multispecies microcosm algal assay procedure, and the latter was found superior as a means of assessing the impact of sodium nitrilotriacetate enrichment since it incorporates environmental and interspecific interactions (Mitchell 1972).

6.3.2 Community Level

The functional response of microbial communities to environmental change is often based on physiological and biochemical activity. The parameters used to measure structural and functional aspects of phytoplankton communities have been reviewed by Berman and Eppley (1974). Techniques for measuring microbial activity are given in Vollenweider (1969a). Sorokin and Kadota (1972), Rodina (1972), and Rosswall (1972).

Changes in physiological activity of microorganisms may be a good measure of environmental impact since they reflect changes in species composition (Grossbard 1972). Sequences of enzyme activity (e.g., nitrification, nitrogen fixation, denitrification) should be studied along with the traditional measurements of respiratory activity. The study of nitrogen metabolism in aquatic systems may be important to impact assessment because many of the enzymatic reactions are sensitive to heat, heavy metals, and dissolved oxygen concentrations, and the analytical techniques involved are fairly well developed (Cairns 1977). He also suggests that differential heterotrophic and autotrophic metabolism of organic and inorganic sulfur might be useful in determining the assimilative capacity of aquatic systems.

Nitrogen fixation in freshwaters has been measured by a number of investigators (Frisch and De 1938; Fogg 1952, 1969; Utterback et al. 1942; Goering and Neess 1964; Stewart et al. 1969; Brezonik and Harper 1969; Howard et al. 1970; Kerin and Brezonik 1971; Horne and Viner 1971; Peterson et al. 1977). Rates of nitrogen fixation have been related to ambient concentrations and chemical forms of nitrogen and phosphorus (Dugdale and Dugdale 1962; Ogawa and Carr 1969; Horne and Goldman 1972; Vanderhoef et al. 1974). Reduced inorganic nitrogen inhibits nitrogenase activity, probably due to negative feedback on enzyme biosynthesis (Fogg 1969), while inorganic phosphorus tends to enhance it. A method for determining available phosphorus concentrations in natural waters was proposed based on nitrogen fixation (acetylene reduction) rates of blue-green algae innoculated into water samples (Stewart et al. 1970). Nitrate reductase activity in marine phytoplankton indicates the use of nitrate as a primary source (Eppley et al. 1969). Glutamic dehydrogenase activity is poorly correlated with ammonium uptake (McCarthy and Eppley 1972).

Several enzymatic techniques have been evaluated for measuring microbial activity in natural communities (Verstaete et al. 1976). Phosphatase activity provides a reliable measure of bacterial and phytoplankton metabolism, saccharase and lipase activity are useful for measuring bacterial metabolism, but amylase activity gives variable results.

The adenylate energy charge ratio (Atkinson 1969)

$$\text{AEC} = \frac{[\text{ATP}] + \tfrac{1}{2}[\text{ADP}]}{[\text{ATP}] + [\text{ADP}] + [\text{AMP}]}$$

where ATP = adenosine triphosphate, ADP = adenosine diphosphate, and AMP = adenosine monophosphate, had recently been used to assess the response of natural populations and communities to stress in aquatic systems. The AEC of an inter-tidal snail was reported to decrease significantly in response to heat, salinity, and hydrocarbon pollutant perturbations; the response was rapid and proportional to the magnitude of perturbation (Ivanovici 1977). Changes in AEC due to perturbation of a natural microbial community may reveal the effects of pollutants (Wiebe and Bancroft 1975). W. J. Wiebe (personal communication) has proposed a theoretical basis for further study of the AEC at the community level:

$$\text{CEC} = \frac{(\text{ATP}_1 + \text{ATP}_2 + \cdots + \text{ATP}_m) + \tfrac{1}{2}(\text{ADP}_1 + \text{ADP}_2 + \cdots + \text{ADP}_m)}{(\text{TA}_1 + \text{TA}_2 + \cdots + \text{TA}_m)}$$

where CEC = community energy charge and TA = total adenylate pool.

Rates of carbon metabolism have been extensively studied in aquatic systems, both directly and indirectly, and provide the basis for determinations of aquatic productivity. Numerous discussions have been devoted to this subject (e.g., Goldman 1965; Strickland and Parsons 1968; Kajak and Hillbricht-Ilkowska 1972; Wetzel 1975; American Public Health Association 1976). Diel changes in dissolved oxygen concentrations have been stoichiometrically equated to photosynthetic carbon fixation and autotrophic and heterotrophic respiration rates. These relationships are incorporated into light/dark bottle techniques (Gaarder and Gran 1927) and plastic dome techniques (Copeland and Duffer 1964; Wetzel 1963) for estimating productivity and respiration in lentic systems. Odum (1956) developed a method for determining productivity and respiration in flowing waters based on diel changes in oxygen concentrations above and below communities of aquatic macrophytes. These methods yield estimates of gross and net productivity and community respiration, but suffer from "bottle effects" in the former cases and diffusion errors in the latter. Standard analysis procedures are given in American Public Health Association (1976).

A modification of the light/dark bottle technique has been developed which incorporates ^{14}C as a tracer of carbon dioxide fixation (Steeman-Nielsen 1952; Strickland and Parsons 1968; American Public Health Association 1976). This technique is thought to measure net productivity (Bunt 1965; Peterson 1978) but organism excretions of labeled organic compounds and cell rupture upon filtration can lead to erroneous estimates (Goldman 1968). Diel changes in dissolved carbon dioxide concentrations resulting from photosynthetic uptake and respiratory release also have been used to measure carbon metabolic rates, especially in microcosm studies (Byers and Odum 1959; Byers 1962). The method relies on pH changes brought about by changes in the bicarbonate-carbonate system as carbon dioxide is utilized or released by organisms. This technique is not useful in highly buffered waters (American Public Health Association 1976) and changes in pH caused by organic excretory products can lead to erroneous estimates of carbon metabolism.

Functional responses of the animal communities to perturbations in aquatic systems have been measured in a variety of ways. Rates of protozoan invasion into polyeurathane foam substrates suspended in the water column were studied in several freshwater lakes (Cairns et al. 1969; Cairns, Boatin, and Younge 1973). Results suggested that the time required for the community to reach equilibrium (colonization rate equal to decolonization rate) was related to the eutrophic state of the lake (Cairns 1977). Zooplankton filtering rates have been shown to respond to changes in environmental conditions, (Buikema 1973; Berman and Heinle 1978) and vertical migration rates have been studied under stressed conditions (Gehrs 1974). Increased fecundity of zooplankton has been observed in lakes overstocked with fish (Hillbricht-Ilkowska 1977).

The migration or drift of stream invertebrates in response to changing conditions of stream flow, light, temperature, and population density has been discussed by Hynes (1970). Sediment loading into natural and artificial streams has been shown to significantly increase invertebrate drift rates (Luedtke 1973; Rosenberg and Wiens 1975; Barton 1977). Gammon (1972) found a linear relationship between suspended stone dust concentrations and invertebrate drift rates and suggested that suspended rather than settled sediments were the probable cause of drift. A positive relationship between current velocity and invertebrate drift rates but not between velocity and drift density was observed in an artificial stream (Ciborowski et al. 1977). Increasing drift density in response to lower discharge rates was seen in a small English stream (Armitage 1977).

Fish brain acetylcholinesterase activity was shown to be depressed by exposure to organophosphate insecticides, the magnitude of depression being a function of chemical concentrations in the water, extent of exposure, and the species of fish (Weiss 1962). Brain acetylcholinesterase activity in fish caught in a South Carolina River receiving waste water from a pesticide manufacturing plant was 46.8 percent lower than that of control fish caught in a nearby uncontaminated river (Williams and Sova 1966). Routine monitoring of fish was proposed as a means of assessing pesticide impacts in aquatic systems. The results of an extensive survey of fish from coastal waters of the southeastern United States suggested that acetylcholinesterase levels less than 90 percent of control levels indicate organic phosphate contamination (Holland et al. 1967).

Growth rates of golden redhorse and bass were significantly impaired by the heavy sediment loading to a stream, but growth of the other fish species studied was apparently unaffected; the latter were less tolerant of the adverse conditions and probably avoided zones of heavy sedimentation (Gammon 1972). Spawning activity of the redhorse was little affected by sediments but sunfish abandoned their nests during periods of intense sediment input. Young-of-the-year trout displayed an increased growth rate in response to nutrient enrichment in several Michigan streams studied by Ball et al. (1973). This study also revealed that fecundity of trout and sculpin populations increased with increasing levels of eutrophication and that the biotic potential of both populations was high at moderate levels, but low at high levels of eutrophication.

6.3.3 Watershed Level

A holistic approach to the study of freshwater ecosystems actually predated many of the approaches discussed above. Forbes (1887) was probably the first to consider lakes as functional entities or "microcosms" with internal webs of components and processes. Naumann (1919) first proposed the "primary economy" system of lake typology based on plant nutrient concentrations, phytoplankton abundance, and sediment types (Brinkhurst 1974). This became the familiar eutrophic-oligotrophic scheme which has received much use and abuse over the years (Brinkhurst 1974; Margalef 1975). Lindeman (1942) pioneered the idea that aquatic systems possess trophic structure organized around the flow of energy and matter. His "trophic dynamic" system has been the basis for numerous models of the energy and material flow through aquatic ecosystems (see Warren 1971; Wiegert 1976). More recently it has been accepted that freshwater ecosystems are not self-contained units but are components of larger watershed systems which often exert commanding influences on internal phenomena (Likens 1972; Fisher and Likens 1973; Hynes 1975; Margalef 1975; Innis et al. 1978). In fact, this idea is a current paradigm in stream research and is fundamental to the analysis of nutrient and sediment impacts.

Trophic State

The trophic state of an aquatic system is an important functional property at the system level of organization (i.e., it is a function of the interaction of the biotic and abiotic processes within the system and the watershed). While trophic state can be defined in several ways, the eutrophic-mesotrophic-oligotrophic scheme based on Naumann's (1919) original lake classification system has been the most widely used. There has been some objection to the use of these terms in a water pollution context since it has been proposed that eutrophication is the sequential course of events in the succession or evolution of lakes rather than simply nutrient enrichment (Brinkhurst 1974; Margalef 1975). In current usage, however, eutrophication (or cultural eutrophication) refers to the process of organic and inorganic nutrient enrichment of lakes or streams and the consequent biotic and abiotic conditions (Likens 1972). This definition is firmly established in the literature and appears to be generally accepted.

A number of biotic and abiotic variables upon which trophic classifications are frequently based are listed in Table 6.5 (Whittaker 1975). Oligotrophic lakes are characterized by relatively low levels of net primary productivity, phytoplankton biomass, chlorophyll a, total organic matter, total phosphorus and inorganic nitrogen, and greater depths of light penetration. The effect of nutrient enrichment is to reverse these trends and shift the system toward eutrophic conditions. These variables are important considerations in assessing nutrient impacts on aquatic ecosystems and several have been used by the National Eutrophication Survey to characterize lakes in the United States (Allum et al. 1977).

A more specific view of trophic state is based on relative magnitudes of primary production and respiration (P/R) occurring within an aquatic system. The P/R ratio is a commonly used measure of autotrophy and heterotrophy. Autotrophic systems are characterized by dominance of primary producers, autochthonous input of organic matter, and P/R greater than one. Heterotrophic systems are driven by allochthonous organic matter, dominated by heterotrophic organisms, and have P/R less than one (Hynes 1970, 1975; Fisher and Likens 1973; Cummins 1975). Many headwater streams and the largest rivers are often heterotrophic while intermediate sized rivers are often autotrophic (Cummins 1975). Inputs of organic matter into autotrophic and heterotrophic systems stimulate growth of heterotrophic organisms (particularly micro-organisms), thus increasing respiration and decreasing P/R.

The ratio of net primary production to biomass (P/B) has been suggested as an effective measure of trophic state in stream ecosystems (Innis et al. 1978). These authors state that in addition to being an indicator of phenological state of community development early in the year or immediately after scouring (P/B is high early relative to later in the year), P/B is an indicator of the extent to which the section being sampled is dependent upon nutritive input from upstream (P/B indicates the relative importance to allochthonous versus autochthonous nutrient inputs. With reference to lakes, Margalef (1975) also has discussed the importance of a ratio of "energy flux to total biomass" as an index of ecosystem state (energy flux might be represented by respiration as well as by net production). As a "global" ecosystem property, this ratio is an "intensive variable and is almost independent of the size of the system."

Nutrient Dynamics

The dynamics of biologically essential elements represent a major functional property of ecosystems. Two components of nutrient dynamics in aquatic systems can be recognized (Likens 1975): 1) nutrient flux is the input and output of materials across system boundaries and is a function of meterologic, geologic, and biologic processes in the system and in the system's watershed

Table 6.5. Some characteristics of types of lakes. (From Whittaker 1975.)

	Oligotrophic	Mesotrophic	Eutrophic	Saline	Dystrophic
Net primary productivity ($g/m^2/yr$)	15-50	50-150	150-500	500-2500	10-100
Phytoplankton biomass (mg/m^3)	20-200	200-600	600-10,000	1000-20,000	20-400
Total organic matter (ppm)	1-5	2-10	10-100	20-200	20-100
Chlorophyll _a_ (ppb)	0.3-3	2-15	10-500	50-1000	0.01-2.0
Light penetration (m)*	20-120	5-40	3-20	2-10	1-5
Total phosphorus (ppb)	<1-5	5-10	10-30	30-100	1-10
Inorganic nitrogen (ppb)	<1-200	200-400	300-650	400-5000	1-200
Total inorganic solutes (ppm)	2-20	10-200	100-500	1000-100,000	5-100

*Estimated depth to which 1% of sunlight penetrates at midday and airshed; 2) nutrient cycling includes all processes within the system whereby nutrients are exchanged among biotic and abiotic components. The "overall structure and function of an aquatic ecosystem are determined by external fluxes and internal cycles." Effects of environmental disturbances on nutrient cycling have not been well documented primarily because processes are not well understood and analytical measurements require the use of radioisotope tracer techniques. A few investigations have been conducted in natural systems (e.g., Hutchinson and Bowen 1950; Rigler 1956), but more detailed studies have utilized simplified aquatic microcosms (e.g., Cushing and Rose 1970; Confer 1972; Sebetich 1975; Howarth and Fisher 1976; Witkamp 1976; Leffler 1977).

The flux of nutrients through aquatic systems has received considerable attention in recent years in the form of mathematical models and input-output budgets. Although modelling is treated in depth in Chapter 6, a few highlights of recent modelling efforts are presented here

The development of mathematical models used for predicting effects of organic and inorganic pollution in lakes and streams has been reviewed (O'Melia 1972). Stream models have been predominantly based on engineering models of the "Streeter-Phelps-O'Conner" type and predict dissolved oxygen and BOD responses to inputs of organic matter. The most commonly used models for lakes are based on the empirical model of Vollenweider (1968, 1969b, 1976) and focus on "critical" inorganic nutrient loading, particularly of nitrogen and phosphorus as related to trophic state. The first model (Vollenweider 1968) predicted critical loading of phosphorus based on mean lake depth but was later improved (Vollenweider 1969b) by the incorporation of coefficients of sedimentation rate and hydraulic residence time. This model was modified by including a coefficient of phosphorus retention used to predict phosphorus concentrations at spring turnover in a number of Canadian lakes (Dillon and Rigler 1974a). The utility of empirical models for predicting the trophic state of lakes was discussed by Dillon and Rigler (1974b) who showed a high correlation between spring total phosphorus and summer chlorophyll a concentrations in several temperate lakes. They suggested that phosphorus loading models combined with the phosphorus/chlorophyll a regression model should be useful for predicting the trophic response of lakes to nutrient enrichment. This idea has been further discussed by Ahl (1975), Jones and Bachman (1975, 1976), Serruya (1975), Chapra and Tarapchak (1976) and Vollenweider (1976), and in general has been supported.

Changes in phosphorus loading models have been proposed which would account for epilimnetic loading of various forms of phosphorus rather than the commonly used values for total lake area or volume and total phosphorus (Schaffner and Oglesby 1978). Such a model (Oglesby and Schaffner 1978) was used to predict the response of phytoplankton standing crop and water transparency in 16 New York lakes to phosphorus loading, and significant correlations with field data were found. The importance of epilimnetic versus total lake volume in phosphorus loading models has been discussed, but it was concluded that the effect of stratification on phosphorus concentration is insignificant compared to the external sources of the element (Schindler 1978).

Analytical simulation models also have been used to predict the response of aquatic systems to nutrient enrichment (e.g., Park et al. 1974; Lehman et al. 1975; Thomann et al. 1975). An ecosystem model of Lake Ontario was compared with two empirical loading models and found to be consistent in predicting annual mean phosphorus and chlorophyll a concentrations (Scavia and Chapra 1977). It was suggested that neither the empirical nor the mechanistic approach is superior to the other; empirical models yield rapid, inexpensive predictions of mean phosphorus or chlorophyll levels from phosphorus loading data, but the mechanistic models provide insight into seasonal dynamics of system components in response to nutrient enrichment.

Construction of input-output budgets of biologically-essential elements represents an integrative approach to the analysis of nutrient impacts on aquatic ecosystems. Budgets for entire drainage basins have shown that disturbances in a watershed (e.g., forest clear-cutting and herbicide treatment) can release large quantities of nutrients, resulting in eutrophication of freshwater streams within the basin (Likens and Borman 1972; also see Likens et al. 1977 for a review of the nutrient budget approach). Expected trends in input-output relationships for essential and non-essential elements, during succession and following perturbation in forested watersheds are shown in Fig. 6.1 (Vitousek 1977). Estimates of nutrient budgets before and after disturbance in a watershed could provide a measure of overall ecosystem response and rate of recovery.

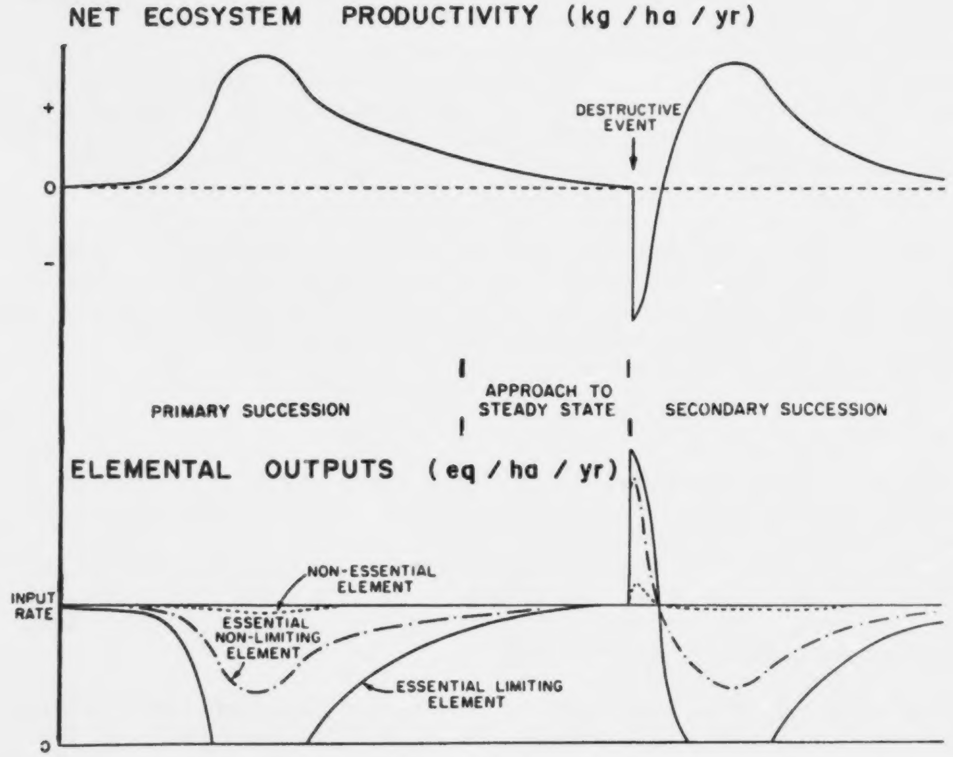

Fig. 6.1. Changes in net ecosystem productivity and elemental losses through time. (From Vitousek 1977.)

Input-output budgets also have been constructed for watersheds containing lakes and impoundments. Johnson and Owen (1971) calculated annual nitrogen and phosphorus budgets for the Bay of Quinte, Lake Ontario and found that 31 percent of the nitrogen and 44 percent of the phosphorus (from industrial, municipal, and tributary stream sources) were retained in the sediments of the bay, reflecting "well-advanced" cultural eutrophication. Studies in Slapy Reservoir, Czechoslovakia, showed significant retention of total phosphorus (as high as 33 percent) but little or no retention of total nitrogen (Prochazkova 1975). N:P ratios in the water column increased from 68 to 137 over ten years, indicating a nitrogen surplus over optimum algal requirements. Budgets were constructed for several elements in the Rawson Lake watershed (Environment Canada, Experimental Lakes Area)(Schindler et al. 1976). Inputs of nitrogen and phosphorus to the lake were rather small (1.0 - 1.5 and 0.05 - 0.10 g/m^2, respectively) and were equally divided between terrestrial and atmospheric sources, while cation inputs were predominantly from tributary streams. The budgets indicated net gains of nitrogen, phosphorus, and chloride, and net losses of seven other ions. The N:P ratio increased from 19.5:1 in the input to 29:1 in the output, giving a retention ratio of 16:1, "very near the expected ratio for phytoplankton." It was suggested that phosphorus limitation is indicated if biological processes predominate over chemical processes in the lake.

Short-term (7 months) and long-term (5 years) budgets for iron and phosphorus were developed in Sedlice Reservoir, Czechoslovakia (Chalupa 1975). Long-term random sampling indicated net accumulations of the elements, but intensive short-term sampling reflected net losses through storm discharges and scouring; the need for proper sampling, statistical analysis, and interpretations of nutrient budgets was emphasized. Others also have suggested the need for constructing budgets over several years to avoid misinterpretations (Schindler et al. 1976; Likens et al. 1977).

At present, the nutrient budget approach to ecosystem analysis probably holds more promise for long-term management than for short-term impact assessment. However, in watersheds where such information is available, effects of proposed activities on nutrient loading and the consequent impacts in freshwater ecosystems might be predictable.

Stability

The concept of ecosystem stability has been a subject of controversy among ecologists for a number of years (see Goodman 1975) and has been demonstrated more as a property of mathematical models than of natural systems. Odum (1969) included stability (resistance to external perturbations) as an attribute of ecosystems, but actual measurements of this property in aquatic systems have been rare. Measurements of stability in terrestrial ecosystems have been discussed by Webster et al. 1975.

A ranking of lakes, rivers, estuaries, and oceans based on their relative "elasticity," inertia," and "environmental stability" has been proposed for environmental impact assessment (Cairns 1977). Ranking orders are as follows: elasticity--rivers>lakes>estuaries>oceans; inertia--estuaries>rivers>lakes> oceans; environmental stability--oceans>lakes>rivers>estuaries. Cairns also proposed a "recovery index" for predicting "the probability of relatively rapid recovery" of a perturbed aquatic ecosystem. The index is based on the following criteria: 1) existence of nearby epicenters for re-invading organisms; 2) transportability or mobility of disseminules; 3) general present condition of habitat following pollutional stress; 4) presence of residual toxicants following pollutional stress; 5) chemical-physical water quality following pollutional stress; 6) management or organizational capabilities for immediate and direct control of damaged area. Recovery implies re-establishment of species originally inhabiting the disturbed area and Cairns reports that the recovery index has been useful in studies of accidental spills and in acid mine drainage.

Ecosystem stability may be quantified based on observations of previously disturbed systems (Westman 1978). Inertia is defined as the ability of a system to resist displacement in structure or function where subjected to a disturbing force, and resilience as the ability of a natural ecosystem to restore its structure following acute or chronic disturbance. Four components of resilience are recognized: 1) elasticity - time required for an ecosystem to return to steady state after disturbance; 2) amplitude - maximum disturbance an ecosystem can sustain and still return to steady state; 3) hysteresis - degree to which pattern of return to steady state is a reversal of pattern of response to disturbance; and 4) malleability - degree to which recovered steady state differs from original steady state. Westman suggests that each of these ecosystem characteristics is measurable and proposes the following criteria. Inertia might be measured as an ecological LD_{50} using a similarity index (i.e., the degree of disturbance resulting in a 50 percent similarity between the before and after disturbance ecosystem). Likewise, elasticity might be measured as the amount of time necessary for 85 percent similarity to be attained between the disturbed ecosystem and "regional climax vegetation" (or perhaps nearby undisturbed lakes or streams in the case of freshwater ecosystems). Where long successional times are involved, computer models might be useful. Amplitude is directly measurable in field experiments, but in practice (i.e., impact analysis) Westman proposes the use of historical data (e.g., aerial photographs) and/or computer models of ecosystems to estimate the frequency of disturbance which "might prevent restoration of the regional climax...." Hysteresis can be measured using non-parametric statistical comparisons of patterns of species disappearance in response to disturbance, and subsequent patterns of recolonization. Malleability might be measured simply as percent similarity between pre-disturbance and post-disturbance stable states of the same ecosystem. Westman suggested that stable state be defined as "a state in which the mean (percent similarity) from each year to the next is no greater than 5 percent over x years and the mean (percent similarity) between the first and the last year in the sequence is no greater than 10 percent."

Values for inertia, elasticity, hysteresis, and malleability appear to be readily calculable from data normally collected in impact analysis of freshwater ecosystems (i.e., species abundance data). At present these measures are descriptive rather than predictive. Westman urges impact assessment investigators to publish results in terms of the above parameters for use in the development of predictive models.

Another view of aquatic ecosystem stability has been stated by Pomeroy

(1975). He compared four types of aquatic systems (two estuarine grass communities, a coral reef, and oceanic plankton) in terms of their relative stability, and concluded that resistance and resilience are a function of the availability of nutrients. Of the systems considered, the intertidal salt marsh is the most resistant and resilient to perturbation due to a large reserve of nutrients in the sediment and a tidal energy subsidy to circulate them. Conversely, planktonic communities, with limited nutrient reserves and no substratum to support and conserve biomass, are the most unstable. Coral reefs appear to have intermediate stability. Of particular relevance to nutrient impact assessment in freshwaters is the idea that naturally enriched systems, which contain species adapted to high nutrient concentrations and abiotic sinks for excess nutrients, are relatively stable with respect to nutrient enrichment. Nutrient-poor systems, on the other hand, have a limited capacity to process excess nutrients and thus, "their only recourse in the presence of [nutrient] pollution is succession, sometimes to an almost entirely different kind of community..." (Pomeroy 1975). Stability in relation to available nutrients is a qualitative and comparative system property but might be estimable in quantitative terms through simulation models of aquatic ecosystems. The concept deserves further research.

6.4 SELECTION OF APPROPRIATE VARIABLES

In conducting an environmental impact analysis or implementing an environmental management scheme, one is confronted with the task of selecting a set of variables which best reflect the response of an ecosystem to disturbance or to various managerial alternatives. Most of the variables reviewed in this chapter are potential candidates for this set in various situations. Thus, given the current state of our understanding of freshwater ecosystems, it appears that a universally applicable set of variables (and response criteria) for nutrient and sediment impact analysis is not attainable and perhaps not even desirable (Verneaux 1976). Spatial heterogeneity across the United States (climatic, geologic, hydrologic, biotic, etc.) creates a wide range of conditions which influence the nature and stress response of freshwater ecosystems, and in a quantitative sense each system is unique. This view, of course, precludes any feasible management strategy. However, a number of features (components and processes) are common to many freshwater ecosystems and have been the basis for classification schemes which aggregate lakes (e.g., Brinkhurst 1974) and streams (e.g., Cummins 1975) into distinct types. Such typologies appear to be necessary for effective management and should be useful in identifying biotic and abiotic variables which are important in certain kinds of ecosystems.

The premise of this report is that the regional scheme integrates many of the factors which account for spatial and temporal variability of freshwater ecosystems, leaving remaining factors to be considered at lower hierarchical levels. The remainder of this chapter 1) examines the biotic and abiotic variables which appear to be most appropriate to the analysis of nutrient and sediment impacts in lotic and lentic ecosystems, and 2) develops a scheme for a hierarchical approach to the analysis of nutrient and sediment impacts. The purpose is not to define a standard set of parameters, but to provide a rational basis for deciding which variables are most likely to be important in particular situations.

6.4.1 Individual and Population Level

At the population and individual levels of organization, nutrient and sediment impacts are best assessed with in situ and laboratory bioassays. Species tolerance and algal nutrient-bioassay procedures are well developed for evaluating direct effects of nutrients and sediment on biota (see section 6.3.1). However, methods for assessing indirect effects are lacking. It is likely that these effects must be considered at higher levels of organization possibly through microcosm or whole system studies.

6.4.2 Community Level

As mentioned earlier, freshwater communities are frequently studied as aggregates of organisms with similar life modes or habitat preferences (Odum's [1971] minor communities). Figure 6.2 (Hellawell 1977) shows the relative emphasis which has been placed on various freshwater communities in river pollution studies, and Table 6.6 (Hellawell 1977) indicates the relative advantages and disadvantages associated with each. Macroinvertebrates and algae have obviously received the most attention, probably because sampling methodologies and taxonomies for these groups are fairly well developed. However, it is important that all of the relevant groups in Figure 6.2 be considered, not as isolated entities, but within the context of the system of which they are a part.

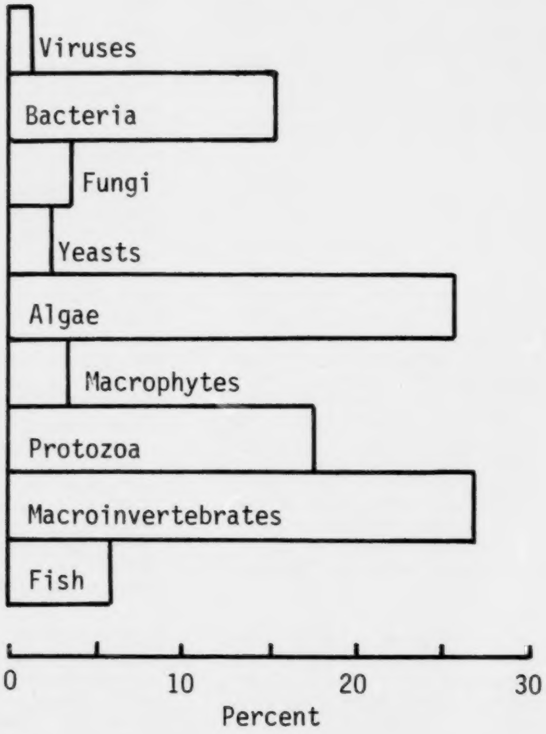

Fig. 6.2. Percentage distribution of taxa recommended for use as indicators based on a literature survey. (From Hellawell 1977.)

Table 6.6. Advantages and disadvantages of different taxa as indicators. (From Hellawell 1977.)

Taxon	Advantages	Disadvantages
Bacteria	Indicators of faecal pollution. Rapid response to environmental changes, including organic and heavy metal pollution. Samples relatively easy to obtain. ROUTINE METHODOLOGY WELL DEVELOPED. Automatic methods for total counts.	Drifting cells--origin not clear, maximum numbers probably downstream of origin of organic pollution. Rapid recovery after intermittent pollution. Need for facilities for sterilizing equipment, plating, incubating, etc. Delay in obtaining results from cultures. Problem of distinguishing dead and living cells in direct counts without special techniques. Is bacteriology of "clean" waters well known? Variability of counts.
Protoza	Supposed rapid response to changes. SAPROBIC VALENCIES WELL DOCUMENTED (e.g., Bick 1968) even within genera, e.g. *Vorticella* (Sladecek, 1971). Gross collection of samples easy.	Taxomonic ability required and good facilities for examination. Some dispute over indicator values since present in "normal" environments. Studies must be quantitative. Drift problems. Variability of microhabitats.
Algae	Useful for eutrophication estimates and sensitivity to turbidity effects (attached forms). POLLUTION TOLERANCES WELL DOCUMENTED, e.g., Fjerdingstad (1964, 1965), Palmer (1969) and several papers by Patrick (e.g., 1954). Automation of counting total numbers.	Not directly useful for heavy organic pollution, nor as indicators of faecal contamination. Not as sensitive to pesticides and heavy metals as other groups. Taxonomic expertise needed. Drift problems with unattached forms. Quantitative sampling difficult for epilithic/epiphytic forms. Counting tedious. Possible rapid recovery of flora. Difficulty in distinguishing living and dead cells in some cases.
Macroinvertebrates	Many sedentary forms--localized effects of pollution detectable. Good keys for several groups. Useful for integration of pollution effects, especially where life history is long. Periodic sampling may therefore be more valid. Qualitative sampling easy. WIDE RANGE OF FORMS AND HABITS--COMMUNITY AS A WHOLE LIKELY TO BE SENSITIVE INDICATOR AND APPLICATION OF NUMERICAL METHODS (SPECIES DIVERSITY INDICES) PROBABLY VALID. Elaborate equipment not required.	Many species drift and may be found in regions where they cannot maintain themselves indefinitely. Groups expected in "poor," and especially lowland, conditions (Chironomids and Oligochaetes) not easily identified. Some groups without adequate keys, e.g., Trichoptera. Absence may be normal part of life cycle--results must be interpreted with care. QUANTITATIVE SAMPLING DIFFICULT. IMPORTANT TO CHOOSE SIMILAR SUBSTRATES WHEN SAMPLING.
Macrophytes	Fixed and relatively easily seen and identified. Good indicators of suspended solid loads. Good indicators of enrichment of soft water.	RESPONSE TO POLLUTION NOT WELL DOCUMENTED (but see Besch and Roberts-Pichette, 1970). Seasonal. Tolerant of intermittent pollution. Poor indicators of enrichment of chalk streams.

Table 6.6. Continued.

Taxon	Advantages	Disadvantages
Fish	INTEGRATORS OF RESPONSES OF FOOD CHAINS AS WELL AS IMMEDIATE EFFECTS ON PHYSIOLOGY. METHODOLOGY WELL DEVELOPED. IDENTIFICATION EASY. Monitored to some extent by anglers.	MOBILE--AVOIDENCE BEHAVIOUR. COLLECTION OF SAMPLES NEEDS MANPOWER.

These community groups also represent functional components of freshwater systems which often are employed, with greater or lesser degrees of aggregations, in ecosystem models. Specification of the couplings (material/energetic) between these components places them in a system context and elucidates biotic variables which require consideration at the community level. The existence of standardized sampling methods and taxonomic keys for several of these groups (e.g., American Public Health Association) simplifies their study and quantification. For the more-poorly studied groups (e.g., bacteria, fungi, yeasts, protozoa), quantitative procedures need further development.

In Chapter 10 a conceptual framework has been developed for the incorporation of community groups into models of standing and flowing water ecosystems. These models recognize spatial heterogeneity of freshwater systems and place communities in appropriate vertical and horizontal strata. Important abiotic factors are also included. Flows and component standing stocks of nutrients (e.g., nitrogen or phosphorus) are used in the models to predict community level effects of nutrient enrichment. Measurements of elemental composition of communities, certain community metabolic activities (e.g., photosynthesis and nitrogen fixation), and feeding transfer rates are necessary for model simulation and impact predictions. While sediments are not explicitly modelled as conservative flows, their impact on communities can be simulated as influences on nutrient dynamics within the model.

6.4.3 Watershed Level

In studies of the effects of stress on ecosystems, Barrett et al. (1976) suggest the study of both structural and functional ecosystem properties. They recommend a "state variable approach" which balances and integrates these properties. In this approach "rate processes" (those involved in energy and matter transfers) are coupled with "state variables" (system components) to form simulation models which predict system behavior through time under the influence of "driving variables" (factors external to the system which are unaffected by system behavior). Odum and Cooley (1976) suggest the study of integrative and interactive system properties in addition to a few "red flag" components which are of special concern in the local situation (e.g., game organisms, endangered species, heavy metals, or organic poisons). Table 6.7 gives their comparison of "standing state" measures, which are often used in freshwater impact assessments, with "dynamic state" measures which might be more appropriate.

A number of watershed level properties are pertinent to nutrient and sediment impact assessments. Since nutrient loading usually has a direct effect on aquatic plants, measurement of variables which reflect primary production should be a first consideration in nutrient impact assessments. The set of variables which defines trophic state (see Table 6.1) includes structural and functional biotic properties as well as relevant abiotic parameters. Several models have been developed for predicting the impact of nutrient enrichment on aquatic primary production (Chapter 7). Indirect impacts of nutrient enrichment are primarily associated with transfers of the excess organic matter produced within the system. Trophic state variables as well as measures of respiration and detrital characteristics reflect these processes.

Table 6.7. Comparison of the structural and functional approaches to the assessment of a body of water. (From Odum and Cooley 1976.)

Standing State Measurements	Dynamic State Measurements
Dissolved Oxygen (D.O.)	Diurnal Oxygen Metabolism
Dissolved Phosphate	Phosphate Turnover Rate
Phytoplankton Biomass	Chlorophyll Concentration (as index to primary production)
List of Species	Indexes of Species Diversity
Density of Fish	Fish Production

Suspended sediment can influence a number of processes and components in freshwater systems, depending on its concentration. These effects are studied at lower levels of organization (organism or population levels). At lower concentrations sediment impacts are usually indirect and are measurable at the system level. Reduced light penetration into the water column inhibits primary production, which in turn reduces overall biotic activity. This is reflected in measures of production and respiration.

6.5 HIERARCHICAL APPROACH TO IMPACT ASSESSMENT

It is implicit in this literature review that freshwater biota can be studied not only at several levels of organization but also at several levels of magnitude as well (e.g., laboratory bioassays, in situ enclosures, whole system studies). In terms of impact assessment, this is consistent with the suggestion of Barrett et al. (1976) that "stress-effect evaluations should include . . . microcosm, seminatural, and natural" systems. These levels are complimentary and observations at one level help to explain phenomena at the other levels. More precisely, these levels of magnitude represent models of the real system of interest and may be physical or abstract (diagrammatic or mathematical) in form. In Figure 6.3 levels of magnitude have been combined with the classification of quantifiable biotic properties from Table 6.1 to form a three-dimensional figure. Each sub-block within the figure represents a set of structural or functional biotic properties at some level of magnitude and organization. Thus, the left, lower, rear sub-block might include an in situ bioassay for studying respiratory activity of a fish exposed to sediment loading, or a dose-response regression model. The right, lower, front sub-block might contain a stability analysis study of a lake system or a nutrient input/output model for the lake.

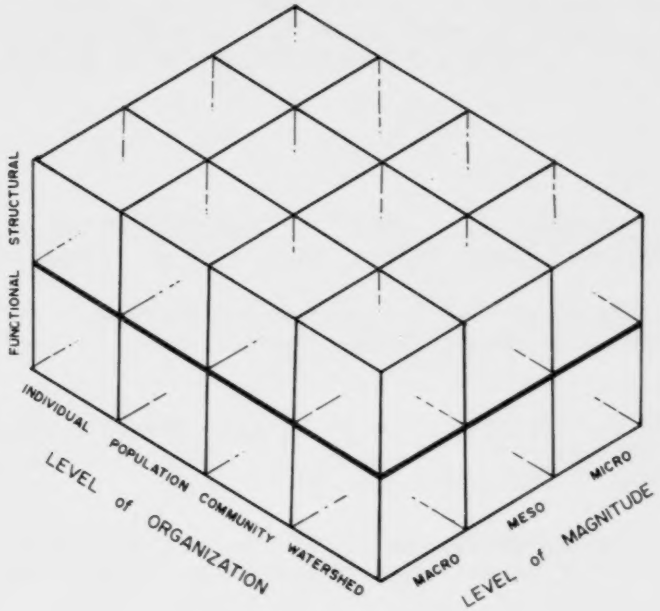

Fig. 6.3. Classification scheme for quantifiable biotic properties.

This scheme provides an integrative framework for structuring impact assessment problems. After initial development of a conceptual model, Fig. 6.3 is entered at the watershed-ecosystem level. Important structural and functional variables are studied in situ to establish "base-line" conditions followed by perturbation studies conducted in enclosures and/or simplified microcosms. Enclosure studies might help identify key species and important variables at the community level. The conceptual model is a guide to selection of community components which should be examined in the field to determine undisturbed conditions (e.g., diversity, biomass, P/R) before perturbation studies are conducted at lower levels of magnitude. "Red flag" species or "species of interest" are studied at the population and organism levels of organization. Abundance and distribution information is gathered in the field and in situ and/or laboratory bioassays establish population and organism tolerances to perturbation. Although the procedure is described as a sequence of events, in practice some of these investigations are conducted simultaneously and not necessarily in the given order. The integrative nature of this scheme lies in the use of information at one level as a guide to further study at the same or other levels. This constant feedback of information is necessary for refinement of conceptual models and keeps teams of investigators in close contact with one another.

This approach recognizes that the nature and stress response of each level of organization is to a large degree dependent on the structure and function of the next higher as well as the next lower level. Thus, impact assessment must be an integrative process to derive a meaningful evaluation of the response of natural systems to human activity. A complete picture can emerge only from studies of structural and functional variables at several levels of organization and magnitude.

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CHAPTER 7

A SURVEY OF AQUATIC ECOSYSTEM MODELLING

7.1 INTRODUCTION

As the interrelations between man and his environment become more intimately related to his survival, there is increasing need to understand ecosystem phenomena in a precise way. The need for mathematical models to predict impact due to nutrient and sediment inputs has become more apparent in the last decade and has resulted in a flurry of activity in ecosystem analysis. Impetus was provided by the International Biological Program, which sponsored numerous modelling programs, and the U.S. Environmental Protection Agency, which endorsed the use of mathematical modelling for impact assessment.

A diversity of models of aquatic systems appears in the literature. Many are aimed at understanding the complexities of ecological systems especially with regard to man's impact. There is a need to initiate discussion about modelling techniques. Such a discussion should promote communication among environmental modellers and provide assessments so managers can evaluate the usefulness of models for particular problems.

A number of conferences and symposia have been held to compare modelling theories and techniques and their application to ecology (Patten 1971, 1972b, 1975b, 1976; Middlebrooks et al. 1973; Innis 1976; Ott 1976). Several journals such as Simulation, Ecological Modelling, and The International Journal of General Systems provide forums for models and modelling techniques. Traditional ecological, limnological, and pollution control journals are more interested in water quality models which more easily fit into traditional scientific format than larger models.

This survey is an attempt to assess aquatic ecosystem models in the literature. Information has been taken from the Survey of Aquatic Ecosystem Models of The Institute of Ecology (Parker and Roop 1974). Only freshwater ecosystem models have been examined; the extensive work on marine coastal ecosystems has not been included. An evaluation of models in terms of usefulness in environmental impact studies will be the primary concern. Particular attention will be given to nitrogen, phosphorus, carbon, and sediment inputs.

7.2 EVALUATION PROCEDURE

Ecosystem modelling is in a state of infancy although it has become increasingly sophisticated; few comprehensive ecological models of aquatic ecosystems have been built. These models are rarely described in the open literature because of their complexity but are found instead in the internal literature of organizations. Many models are incomplete because they take so long to build and are constantly evolving. The modelling and simulation of aquatic ecosystems is a complicated undertaking with many considerations involved. Criteria used to evaluate models and modelling philosophy are discussed below.

7.2.1 Objectives and Philosophy

The major purpose of ecosystem models is to account for and explain observed behavior of ecosystem properties. The variability accounted for by a model is related to the precision of the model; a model which describes more observed system variability is more precise. Coarse resolution models use a small set of parameters which account for most of the observed variation. Fine resolution models use a larger set of variables which potentially account for more observed variation and predict with greater precision or explain in greater detail. The number of variables used in a model is usually limited by bounds set by economy and practicality. It is advantageous to use a small set which can be obtained with a minimum of effort and expense yet still meet the required standards of precision or explanation. Explanatory models are sometimes neither the simplest nor the most efficient models.

Ultimately a model can be judged only as to whether it meets a priori objectives. A primary objective considered in models discussed here is to predict the effects of nutrient and sediment perturbations in aquatic ecosystems. The ability to predict system response can be assessed either in qualitative or quantitative terms. A second goal of ecosystem modelling important to impact assessment is to communicate a holistic or macroscopic ecosystem perspective. Ecological, political, and social managers often must be made to think in terms of ecosystems rather than in terms of isolated components and events. A third objective of many aquatic ecosystem models is to provide and evaluate hypotheses about ecosystem structure and behavior. Models, being hypotheses concerned with the nature of ecosystems and ecosystem behavior, need to be tested and contrasted with opposing ecosystem hypotheses. An evolving course will gradually emerge representing a compromise among different theories.

7.2.2 Generality

Several models are meant to be general ecosystem paradigms which are potentially applicable to a wide vareity of ecosystems. Although much information used in ecological models is obtained from general ecological literature (Overton 1977), site specific data are often required to calibrate a model. The best way to evaluate the generality of a model is to enumerate the systems where the model has been applied.

7.2.3 Level of Resolution

Models of aquatic ecosystems can be classified at several levels of resolution. Coarse resolution water quality models deal with macroscopic properties of systems (e.g., mean depth, volume, flow rate, retention time) and predict variables such as dissolved oxygen, dissolved phosphorus, and/or chlorophyll concentrations. At the other end of the spectrum are fine resolution models which involve and predict properties of ecological components and their interactions. Fine resolution models are potentially capable of predicting dynamic ecosystem properties with greater precision than coarse resolution models (Scavia and Chapra 1977). The required level of resolution depends on questions being asked of the system and the needed precision of the answers.

7.2.4 Model Structure

Components and interactions demonstrate the dependency network of systems by describing the paths over which cause and effect travel (Hutchinson 1948; Caswell et al. 1972; Patten et al. 1976). Biotic, chemical, and physical components can be regarded as propagators of cause. In fine resolution models the internal cause and effect structure may be identified in great detail.

Compartments and State Variables

Compartments often represent stores of conservative materials such as energy, biomass, numbers of organisms, nitrogen, phosphorus, or carbon. State variables describe properties of physical, chemical, and biological compartments. Usually only a few properties are simulated in a single model because of the complexity introduced by modelling large numbers of properties (Bierman et al. 1973). As indicated in Chapter 5, some biotic compartments have been used in a majority of nutrient and sediment impact studies and in ecological models. These compartments have been selected on the basis of usefulness for field research and their ability to assess impact.

Interactions

Prevailing ecosystem paradigms indicate that many processes are basic to ecosystems: nutrient cycling, primary production, herbivory, carnivory, decomposition, detritivory, etc. (E. P. Odum 1971). Mathematical formulations and coefficient values which describe interactions vary between models, such as in the nutrient limitation of phytoplankton (Park et al. 1978). The mathematical form may not be as important as the existence of the ecological relationship, especially in a system near steady state. Model behavior is largely determined by network structure and coefficient formulations which describe the dependency structure in an ecosystem (Hill and Durham 1978; Hill 1979).

Several mathematical formats have been used for modelling aquatic ecosystems. When differential or difference equations are used to describe behavior of ecosystems, relationships among components are assumed to be deterministic. Stochastic models of ecosystems have also been constructed (Parker 1974; Abendt 1975; Barber 1978a, 1978b). Discussions of stochastic versus deterministic models can be found in Wiegert (1975a), and Parker (1974).

Many models are modular, having been built in terms of submodels which are then brought together. The usefulness of the modular approach for constructing systems is pointed out in the watchmaker's parable of Simon (1973).

The watchmaker's work is facilitated by building 10 subcomponents consisting of 10 parts each and then putting these subcomponents together, rather than building the whole directly from 100 parts. Modularity allows flexibility in adding or modifying components when components are built to fit together.

Inflows and Terrestrial-Aquatic Coupling

Aquatic ecosystems are open to their environments and are driven by allochthonous carbon and nutrient inputs (Hynes 1970; Boling et al. 1975; Cummins 1975; Wetzel 1975). The importance of the watershed in determining the behavior of aquatic ecosystems has been the focus of contemporary ecological research (Likens and Borman 1972; Schindler et al. 1976). Although ecologists have studied nutrient relationships between watersheds and aquatic systems, no comprehensive ecological model has been built which unites a watershed model with an aquatic ecosystem model. Establishing the terrestrial-aquatic link is an important direction that modelling must take.

Outflows

Outflows are as important in determining the properties of aquatic ecosystems as inflows. Tributary outflow, harvesting, evapotranspiration, sedimentation, and groundwater seepage are important to ecosystem behavior. Rivers and streams are flow-through systems by definition; lakes are impoundments for drainage systems but generally have outflows.

Controls

Various physical and chemical factors constrain and often drive the behavior of aquatic ecosystems and their components. Temperature, circulation, turbidity, and pH are some of the controls which are simulated in aquatic ecosystem models.

Spatial Considerations

The spatial structure of aquatic ecosystems is important in determining ecosystem behavior. Reaches of a stream vary with flow rates, substrate type, watershed type, etc. (Hynes 1970). Spatial diversity in lakes and reservoirs can influence system behavior (Vollenweider 1968; O'Melia 1972; Vollenweider and Dillon 1974; Oglesby and Schaffner 1978). The spatial structure of streams and rivers is different from lakes and reservoirs and helps to account for their different behaviors.

Systems Analysis and Simulation

Systems analysis techniques provide a basis for assessing model behavior and generating new hypotheses about ecosystem structure and behavior. Simulation and perturbation trials, sensitivity analyses, network analyses, flow analyses, and model aggregation or condensation are techniques which have management implications. Model validation or verification also must be considered with systems analysis techniques. As statements about real ecosystems, models should be assessed in terms of real world behavior, that is, they need to be validated. Formal statistical techniques often are not useful for validating ecosystem models (Wiegert 1975a; Innis 1976; Mankin et al. 1977). Less formal qualitative techniques, such as comparison or corroboration of calculated results with observed results, often are used to validate models (Caswell 1976).

7.3 MODEL EVALUATIONS

A summary of models in the literature detailing the points discussed above is presented in Table 7.1. Detailed evaluation of eight major aquatic ecosystem modelling approaches follows this. These approaches include coarse resolution water quality models which are assessed first (section 7.3.1). Then several models which involve a fine level of resolution are examined: the Eastern Deciduous Forest Biome lake models, the Manhattan College models of the Great Lakes, the ecological model, Coniferous Forest Biome stream models, the energy circuit language, and the linear modelling approach used in Lake Texoma Cove (sections 7.3.2 - 7.3.7).

7.3.1 Coarse Resolution Water Quality Models

Coarse resolution water quality models are used to rapidly assess ecosystem productivity and impact of nutrient loading with a few easily measured parameters. Several major references on the coarse resolution water quality models exist (O'Connor 1961; Vollenweider 1968, 1972, 1975; O'Connor and Mueller 1970; O'Melia 1972; Vollenweider and Dillon 1974; Abendt 1975; Oglesby and Schaffner 1978; Schaffner and Oglesby 1978; Schindler 1978).

Objectives and Philosophy

The primary objective of these models is to predict or explain water quality changes resulting from pollution or nutrient loading (Vollenweider and Dillon 1974). Another objective is to establish criteria for tolerable and critical loadings based on easily measured parameters. Water quality models provide a framework for comparing nutrient loading and water quality relationships in a large number of aquatic ecosystems. Some models predict recovery time of a lake after nutrient diversion (Dingman and Johnson 1971; Cooke et al. 1973; Emery et al. 1973).

Generality

Water quality models are relatively simple and applicable to a wide range of lakes and streams. Vollenweider-type lake models have been applied to a number of situations in North America and Europe but have been restricted to well-mixed bodies of water studied in classic limnology (Sonzogni and Lee 1972). Spatially diverse systems such as marshes, swamps, and shallow littoral lakes are not handled well. Models which predict biological oxygen demand (BOD) have been applied to a number of streams and rivers throughout the United States (O'Melia 1972).

Although coarse resolution models are theoretically useful for any nutrient, they usually have been used for oxygen in streams and phosphorus in lakes. Carbon and chlorides also have been modelled using this approach

Table 7.1. A survey of aquatic ecosystem models with characteristics related to ability to predict impact.

MODEL REFERENCE	SYSTEM	REGION	SPATIAL PARTITIONS	AQUATIC TERRESTRIAL INTERACTIONS	TYPE		WATERSHED INPUTS				CHEMICAL COMPONENTS				BIOTIC COMPONENTS						
					REGRESSION	SIMULATION	N	P	C	SEDIMENT	POM	DOM	OXYGEN	CHLOROPHYLL	MACROPHYTES	ALGAE	MACROFAUNA	MICROFAUNA	FISH	DECOMPOSERS	MISCEL.
Abendt 1975	Stream	General	None			X			X				X								
Bloomfield et al. 1973 Park 1974	Lake George	New York Division 21	Pelagic Regions/ Sediments	Nutrient Loading Data		X	X	X	X	X	X	X	X		X	X	X	X	X	X	
Boling 1974	August Creek	Michigan Division 22	None	Time Varying Inputs		X					X	X					X			X	
Brandes et al. 1973	Tellico Reservoir	Tennessee Division 22	Interconnected Spatial Sections	Hydrology and Waste Input		X	X	X	X	X	X	X	X			X	X	X	X	X	
Brylinski and Mann 1973	IBP Lakes		None	None	X		X	X				X		X		X	X	X			
Chapra 1979	Saginaw Bay	Michigan Division 22	None	Nutrient Loadings		X		X													
Chen 1971	Reservoirs	California	Interconnected Spatial Sections	Hydrology and Waste Input		X	X	X	X	X	X	X	X			X	X	X	X	X	
Chen and Orlob 1972	Lake Koocanusa	Montana Division 31	Interconnected Spatial Sections	Hydrology and Waste Input		X	X	X	X	X	X	X	X			X	X	X	X	X	
Chen and Orlob 1972	Puget Sound	Washington Division 24	Interconnected Spatial Sections	Hydrology and Waste Input		X	X	X	X	X	X	X	X			X	X	X	X	X	
Chen and Orlob 1975	Lake Washington	Washington Division 24	Interconnected Spatial Sections	Hydrology and Waste Input		X	X	X	X	X	X	X	X			X	X	X	X	X	
Cooke et al. 1973	Twin Lakes	Ohio Division 22	Littoral, Epi-, Meta-, Hypolimnion, Sediments	Watershed Input		X		X							X						

Table 7.1. (Continued)

MODEL REFERENCE	SYSTEM	REGION	SPATIAL PARTITIONS	AQUATIC TERRESTRIAL INTERACTIONS	TYPE		WATERSHED INPUTS				CHEMICAL COMPONENTS				BIOTIC COMPONENTS						
					REGRESSION	SIMULATION	N	P	C	SEDIMENT	POM	DOM	OXYGEN	CHLOROPHYLL	MACROPHYTES	ALGAE	MACROFAUNA	MICROFAUNA	FISH	DECOMPOSERS	MISCEL.
Correll 1974	Rhode River	Maryland Division 23		Watershed-Estuary		X	X	X	X	X	X	X	X		X	X	X	X	X	X	
Dettmann 1974	Lake Wingra	Wisconsin Division 22	Pelagial			X	X	X			X	X				X	X	X	X	X	
Dillon and Rigler 1974	Lakes	Northern U.S.	None	Constant P Loading	X			X						X							
Gayle 1975	Lake Okeechobee	Florida Division 23	Marsh, Pelagic Regions, Sediment	Waste Input		X		X			X	X	X			X					
Gilliland 1975	Peninsular Florida Peace River	Florida Division 23	Peninsular Florida Peace River	P mining, wastes from watershed		X	X	X						X		X					
Glanz 1972	Blue Marsh Reservoir	Pennsylvania	Interconnected Spatial Sections	Hydrology and Waste Input		X	X	X	X	X	X	X	X			X	X	X	X	X	
Glanz et al. 1972	Tock Island Dam	New Jersey	Interconnected Spatial Sections	Hydrology and Waste Input		X	X	X	X	X	X	X	X			X	X	X	X	X	
Glanz and Orlob 1973	Lincoln Lake	Illinois Division 25	Interconnected Spatial Sections	Hydrology and Waste Input		X	X	X	X	X	X	X	X			X	X	X	X	X	
Hall 1974	Flax Pond Estuary	New York Division 22				X	X	X							X	X	X	X	X	X	
Huff et al. 1973	Lake Wingra	Wisconsin Division 22	Pelagic Region	Hydrologic Transport Model, Nutrient Loading		X	X	X	X		X	X				X	X	X	X	X	
Kadlec 1978	Houghton Lake Marsh	Michigan Division 21	Interconnected Spatial Sections	Sewage Input		X	X	X	X	X	X	X			X	X					

Table 7.1. (Continued)

MODEL REFERENCE	SYSTEM	REGION	SPATIAL PARTITIONS	AQUATIC TERRESTRIAL INTERACTIONS	TYPE		WATERSHED INPUTS				CHEMICAL COMPONENTS				BIOTIC COMPONENTS						
					REGRESSION	SIMULATION	N	P	C	SEDIMENT	POM	DOM	OXYGEN	CHLOROPHYLL	MACROPHYTES	ALGAE	MACROFAUNA	MICROFAUNA	FISH	DECOMPOSERS	MISCEL.
King 1973	Trinity River																				
MacCormick et al. 1972	Lake Wingra	Wisconsin Division 22	Pelagic Region													X	X	X	X	X	
Marshall et al. 1976	Beaver River Basin	Ohio, Pennsylvania Division 22	River Junctions, Stretches, Headwater Reaches	Watershed Input		X	X		X				X								
McIntyre and Colby 1978	Oregon Streams	Oregon	None	Watershed Input		X			X		X	X				X	X			X	
O'Connor and Dobbins 1958	Stream		None	Pollutant Input									X								
Odum 1978	Cypress Swamp	Florida Division 23	Watershed, Cypress Dome	Sewage Input		X	X	X													
Oglesby and Schaffner 1978 Schaffner and Oglesby 1978	Lakes	New York Division 21		Constant P Loadings	X			X						X							
O'Melia 1972	Lakes	Europe	Epi-, Hypolimnion, Sediment	Constant P and C Loading		X		X	X												
Parker 1974	Libby Lake	Wyoming Division 21				X			X							X	X	X	X	X	
Patten et al. 1975	Lake Texoma Cove	Oklahoma-Texas Division 25	None	Time Varying Inputs		X	X	X	X	X	X	X	X		X	X	X	X	X	X	X
Rich 1974	Dunham Pond	Connecticut	Watershed Model						X		X	X	X		X	X		X		X	

Table 7.1. (Continued)

MODEL REFERENCE	SYSTEM	REGION	SPATIAL PARTITIONS	AQUATIC TERRESTRIAL INTERACTIONS	TYPE		WATERSHED INPUTS				CHEMICAL COMPONENTS				BIOTIC COMPONENTS						
					REGRESSION	SIMULATION	N	P	C	SEDIMENT	POM	DOM	OXYGEN	CHLOROPHYLL	MACROPHYTES	ALGAE	MACROFAUNA	MICROFAUNA	FISH	DECOMPOSERS	MISCEL.
Scavia et al. 1976a, 1976b	Lake Ontario Great Lakes	Division 22	Epi-, Hypo-limnion	Constant P Loading		X	X	X	X		X	X		X		X	X	X			
Schindler 1978	IBP Lakes		None	None	X		X	X				X		X		X	X	X			
Shannon and Brezonik 1972	Lakes	Florida Division 23	None	Watershed Characteristics	X		X	X													
Streeter and Phelps 1925	Ohio River	Division 22		Pollutant Input									X								
Vollenweider 1968, 1969	Lakes	Northern U.S., Europe	None	Constant P Input	X			X													
Vollenweider 1972, 1975	Lakes	Northern U.S., Europe	None	Constant P Loading		X		X													
Walters 1974	IBP Lakes and Watersheds					X									X	X	X	X	X	X	
Waring 1974	Streams in Watershed	Oregon													X	X	X	X	X	X	
Whitehead and Young 1974	Stream	Europe	None			X			X				X								
Wlosinski 1974	Stream	Utah Division 31				X	X	X	X						X	X	X	X	X	X	

(O'Connor and Mueller 1970; O'Melia 1972).

Level of Resolution

Water quality models use and predict whole ecosystem properties such as total phosphorus and will not answer dynamic or detailed questions about ecological components or interactions. Most lake models are calibrated on an annual time scale, predict annual system properties, and require measurements one or two times a year. The most useful time scale for prediction and measurement may not be a year; instead a "limnological year," having a length which varies with meteorological, hydrological, and geological conditions may be defined (Cooke et al. 1973). River models often are calibrated on a shorter time scale and predict properties at points in space and time, downstream from point of pollution loading.

Model Structure

Three basic types of coarse resolution models exist: regression, correlation, and simulation models. Regression models of streams predict biological oxygen demand or dissolved oxygen using pollution loading and stream flow, width, depth, and cross-sectional area. Regression models of lakes predict trophic state and nutrient concentrations using nutrient loadings and system parameters such as depth, retention time, and area. Correlative models examine the relationships between several variables such as nutrient concentrations and chlorophyll concentrations (Brylinsky and Mann 1973; Dillon and Rigler 1974; Oglesby and Schaffner 1978; Schindler 1978). Correlative models theoretically should not be used for prediction. Simulation models include differential, difference, or stochastic equation models which predict nutrient concentrations or trophic state on the basis of system inputs, outputs, and processes affecting concentrations (O'Melia 1972; Vollenweider 1972, 1975; Vollenweider and Dillon 1974; Whitehead and Young 1974). Inputs are from the watershed, the atmosphere, and the sediments; outputs are to outflow, the atmosphere, and the sediments. Refinements include loss to sediments, atmospheric invasion, chemical reactions, internal recycling by biota and sediments, and time-varying inputs.

Consideration of spatial heterogeneity in coarse resolution models can account for some of the variation in observed ecosystem behavior. Variation in lake behavior can be explained by considering the littoral zone and shoreline (Vollenweider 1968). Vertical stratification is important in many lakes and can be included in water quality models (O'Melia 1972; Huff et al. 1973; Dillon 1974; Oglesby and Schaffner 1978).

The ability of models to predict impact depends on the quality of nutrient loading measurement. Measurement of nutrient loading is often difficult because of numerous and diffuse sources, and time-varying input data may be required to make valid predictions (O'Melia 1972; Sonzogni and Lee 1972; Cooke et al. 1973) making necessary more data and larger sampling programs. Phosphorus loading can be estimated on the basis of watershed characteristics (Patalas 1972; Shannon and Brezonik 1972; Cooke et al. 1973; Patalas and Salki 1973; Vollenweider and Dillon 1974), and drainage area, geology, land use, and population have been suggested as influencing characteristics

(Cooke et al. 1973; Vollenweider and Dillon 1974; Dillon and Kirchner 1975).

Systems Analysis and Simulation

Because of their simplicity and small data requirements, coarse resolution water quality models can be easily validated. Correlations between model parameters and ecosystem properties such as chlorophyll, trophic state, and phosphorus concentrations are often high (Brylinski and Mann 1973; Vollenweider and Dillon 1974; Schindler 1978). Simple input-output water quality models are compatible with statistical validation procedures (Abendt 1975).

Assessment

Coarse resolution water quality models provide a quick and useful way of assessing pollution in streams and eutrophication in lakes; however, these models are not as inherently precise as fine resolution models, and they generally do not predict dynamic properties. Only well-mixed systems can be adequately described by the simpler models. Structurally complex systems can be modelled by adding terms representing spatial heterogeneity. Nutrient loadings (especially nitrogen) need to be better characterized in terms of watershed properties, variation with time, and sediment and biotic regeneration. Phosphorus-chlorophyll correlation models are indirectly related to phosphorus loading and their usefulness in predicting impact should be evaluated.

7.3.2 Eastern Deciduous Forest Biome (EDFB) Aquatic Ecosystem Models

The initial Eastern Deciduous Forest Biome model was the Comprehensive Lake Ecosystem Analyzer (CLEAN) which was intended to be a model framework for incorporation of other work done in the Eastern Deciduous Forest Biome. CLEAN has evolved into the more recent models CLEANER AND MS. CLEANER. Comprehensive modelling and field research was done at two sites within the Eastern Deciduous Forest: Lake George, New York and Lake Wingra, Wisconsin. Coordination between the two sites was accomplished by a multidisciplinary research team, which established close relationships between modellers and field researchers. Documentation for CLEAN can be found in Park and Wilkinson (1970, 1971), Park et al. (1972), and Park et al. (1974); for CLEANER in Scavia (1974), Bloomfield et al. (1975), Park et al. (1975), Scavia and Park (1976), and Clesceri et al. (1977); and for MS. CLEANER in Groden (1977), Desormeau (1978), Park et al. (1978, 1979).

Objectives and Philosophy

The central objective of the modelling program has been to understand better ecosystem dynamics. An effort was made to include as much biological and ecological realism as possible. A second objective was to predict the consequences of man-induced perturbations. Thirdly, the modelling program was to couple all generalized aquatic process models developed in the Biome.

Generality

CLEAN, CLEANER, AND MS. CLEANER were built to be used at either

Lake George or Lake Wingra which represent "different ends of the environmental continua." The models were intended to be flexible enough to model other ecosystems as well. A number of European lakes have been modelled with MS. CLEANER (Park et al.1978). Many ecological formulations used in these models are general; a terrestrial ecosystem energy model described by O'Neill et al. (1972) was the source of many formulations used in the models (Bloomfield et al. 1973).

Level of Resolution

Models and submodels were constructed at several levels of resolution. CLEAN, CLEANER, and MS. CLEANER compromise generalized process submodels which represent basic ecological interactions occurring within aquatic ecosystems. A number of fine resolution submodels were built to simulate detailed processes, which are used when precise results are needed. CLEAN consists of 28 compartments and operates for a year with time steps of one day or less. MS. CLEANER consists of up to 20 biotic state variables and 20 abiotic state variables in each of 10 spatial segments; it is rarely run in its entirety because of its complexity. Because simulations are expensive and time consuming, it is advantageous to use as little of the model as possible to adequately answer questions. As few as two state variables have been used in a simulation (Park et al. 1978).

Model Structure

Components in MS. CLEANER potentially include phytoplankton (4 types), submersed aquatic macrophytes (4 types), zooplankton (5 types), fish (2 or more types), bottom animals (2 types), bacteria and fungi (3 types), DOM (7 types), POM (4 types), inorganic nutrients (5 types), dissolved oxygen, and inorganic carbon (3 types). Mass or biomass is used to describe most compartments. However, because age structure affects the behavior of some biotic components, numbers of organisms can be used simultaneously with mass. Other components can be added as needed.

Coefficients for equations were determined by experimental research. Most interactions between components are nonlinear. The basic models have evolved as various subsystems were created, tested, calibrated, and coupled with the central model framework. The modular framework facilitates model evolution.

Nutrient interactions were not included in the initial formulations of CLEAN (Bloomfield et al. 1973); instead, nitrogen and phosphorus were used as forcing functions rather than state variables. During evolution of the models, nutrients were included and nutrient interactions with biota, organic materials and decomposers became increasingly sophisticated. Development of nutrient interactions hinged on a decomposition submodel (Clesceri et al. 1977). Arguments for various nutrient limitation formulations are expressed in Bloomfield et al. (1973), Scavia and Park (1976), and Park et al. (1978). Internal pools of nutrients in phytoplankton are used to give realistic simulations (Park et al. 1978). Adaptive characteristics of multispecies-phytoplankton communities are included in the nutrient limitation characteristics (Scavia and Park 1976; Groden 1977; Park et al. 1978). Incident solar radiation, water temperature, wind or barometric pressure, allochthonous dissolved and particulate organic matter, water circulation, and nutrient loadings are driving variables.

CLEAN is a point model which describes average conditions for a square meter of lake surface. In order to describe processes which occur in different parts of a lake, the point model is calibrated to conditions at each part of the lake. MS. CLEANER can describe spatial heterogeneity with 10 spatial segments which are interconnected via mass flows. These segments simulate horizontal and vertical diversity within an aquatic ecosystem. Inclusion of all 10 spatial segments is expensive and unwieldy.

No explicit attempt has been made to couple a watershed model with the basic aquatic ecosystem models. A Hydrologic Transport Model (HTM) was developed at the Lake Wingra site (Huff 1968) which predicts nutrient runoff with various land use practices. Potentially this and other watershed models can be coupled with the basic aquatic ecosystem models but would greatly add to computer time and expense.

Systems Analysis and Simulation

Verification of model behavior has been done by comparing calculated values with observed values. Perturbation and sensitivity analyses have been done with MS. CLEANER in order to better assess model behavior. Interactive programming allows one to perturb coefficients, loadings, and state variables. Sensitivity analyses can be done with a submodel, which introduces random perturbations of varying magnitudes.

Assessment

The CLEAN, CLEANER, and MS. CLEANER series is the most elaborate aquatic ecosystem modelling program attempted. The models contain a large degree of ecological realism; the most recent versions of MS. CLEANER contain provisions for evaluating "nutrient enrichment, thermal pollution, siltation, impoundment, and fish removal" (Park et al. 1978). These models are expensive and time consuming to run because of their complexity; however, modular construction allows researchers to solve only portions of each model to answer specific questions.

7.3.3 Phytoplankton-Zooplankton-Nutrient Interaction Models of Manhattan College

A modelling approach which has been applied to the Great Lakes and various estuaries is that developed by DiToro, Thomann, O'Connor, and Mancini of Manhattan College and Hydroscience, Inc. Models derived from this approach simulate the dynamics of phytoplankton chlorophyll, zooplankton carbon, and various forms of nitrogen and phosphorus. Documentation can be found in DiToro et al. (1971), Thomann et al. (1974), and DiToro et al. (1975).

Objectives and Philosophy

This modelling approach uses chemical kinetic laws and mass transport processes. Detailed chemical and physical descriptions of this philosophy can be found in DiToro (1974, 1976). Objectives include determination of important interactions in lake eutrophication, analysis of lake water quality, and biological response to natural and man-made inputs, and estimation of the direction of change expected with environmental control actions.

Level of Resolution

The models described in Thomann et al. (1974) and DiToro et al. (1975) are at an intermediate level of resolution. Spatial and temporal distribution of water quality parameters is predicted on a seasonal basis. Models are run for at least a year and for up to 10 years.

Generality

The interactions between biotic and chemical compartments are represented in general form and should be applicable to many lakes. Values of model variables often are taken from the general literature (Thomann et al. 1974) and then are adjusted to fine tune the models to data sets. The models have been applied to Lake Ontario, Lake Erie, and Lake Huron. Similar models have been applied to the Sacramento-San Joaquin Delta and Potomac estuaries (O'Connor et al. 1972; DiToro et al. 1977). Phytoplankton and zooplankton behaviors are simulated but fish, macrophyte, and benthic invertebrate behaviors are not. Organic nitrogen, ammonia, nitrate, organic phosphorus, and orthophosphate are chemical forms which have been simulated. Silica and oxygen are included in the estuary models (DiToro et al. 1977) and can be incorporated into the lake models.

Model Structure

Each model is a set of nonlinear differential equations which describe the chemical kinetic relations among biotic and chemical compartments. Nutrient limitations of phytoplankton are formulated as Michaelis-Menten interactions. Spatial segments, which are assumed to be well-mixed, simulate horizontal and vertical heterogeneity within lakes. Although 60-100 segments potentially can be used in a model, the number and properties of horizontal segments vary according to the lake and the model objectives; the Lake Ontario model (Thomann et al. 1974) included only vertical segments, whereas the Lake Erie model (DiToro et al. 1975) included 4 horizontal and 3 vertical segments. Arrangement of spatial segments depends on circulation patterns, basin topography, and inputs from the watershed. Movement of nutrients, phytoplankton, and zooplankton through a lake are described as physical, advective, and dispersive processes between the spatial segments.

Simulation and Systems Analysis

Validation of the models has been done by comparing calculated values with observed values. Qualitative judgements were used for validation; calculated values were described as being in reasonable agreement with observations.

Assessment

Good prediction of phytoplankton chlorophyll, zooplankton carbon, phosphorus, and nitrogen values have been obtained for several of the Great Lakes and estuaries. Phytoplankton chlorophyll, as predicted by these models, lags behind observed values, perhaps because internal phytoplankton pools of nutrients were not incorporated (Park et al. 1978). These models will not predict behavior of poorly mixed systems such as marshes and littoral zones. They do not include fish, macrophytes, and benthic animals, which are important to nutrient dynamics in many lakes.

7.3.4 Chen and Orlob's Ecological Model

The ecological model of Chen and Orlob has been used for a number of systems across the country and has been shown to predict successfully. The most comprehensive application of the model was done for Lake Washington, Washington, for which Edmondson's (1961, 1969, 1972) extensive data set was available. Documentation of the modelling approach can be found in Chen (1970) and Chen and Orlob (1968, 1975).

Objectives and Philosophy

The modelling approach integrates fundamental physical, chemical, and biological principles in aquatic ecosystems so all pertinent parameters and processes are coupled. One objective is to simulate ecological processes in water resources systems and to enable engineers and planners to use ecological information in management of water projects. The model should allow realistic assignment of priorities for pollution control, guide design of water quality sampling programs, and identify problem areas for research.

Generality

Separate models have been built for a number of lakes, reservoirs, and estuaries in the United States (Parker and Roop 1974). Much of the information required to calibrate this model is site specific and includes: system geometry, physical and chemical water characteristics, weather conditions, hydrology, waste loads, historic water qualities, fish stock, and fish harvest. Ecological information used in the model is general and can be obtained from the literature.

Level of Resolution

The model represents a fine resolution approach which can address specific questions about biota, and spatial and temporal distribution of chemical parameters. Output of system parameters can either be a synopsis at a point in time or trajectories of properties through time. Time steps vary from 3 - 4 hours to 15 day periods, and the model may be run for up to a year.

Model Structure

Components, inputs, and outputs are described by mass, mass balance equations, and mass transference equations. The basic processes modelled are chemical reactions, inflow, outflow, advection, diffusion, sedimentation, and exchange. Life forms used in the model are fish, bacteria, phytoplankton, zooplankton, fish, and benthic animals. Carbon, phosphorus, and various forms of nitrogen are among the water quality parameters predicted. Other physicochemical components used in the model are alkalinity, pH, benthic detritus, temperature, and toxicity.

Various portions of a lake, reservoir, or estuary are simulated by interconnected cells which represent well-mixed portions of space. Cells are connected by equations which describe transfer of mass. Vertical stratification is represented by layers of horizontal cells, and lake circulation due to thermal conditions and meteorological input is stimulated

Real data are used to drive the model. Nutrient loadings to the system are dealt with as time varying point sources in the same manner as tributaries. Watershed characteristics are not used in the model. In aquatic ecosystems where major inputs are diffuse, such as from ground water or direct surface runoff, the model as presented in Chen and Orlob (1975) may not work well.

Simulation and Systems Analysis

Validation has been done by comparing calculated values to observed values. In the case of Lake Washington, the data sets are extensive and the models predict the effects of nutrient diversion.

Assessment

The Chen and Orlob ecologic model deals with both spatial and temporal heterogeneity in chemical and biotic components. The model can address specific and general questions about impacts of nitrogen, phosphorus, carbon, and sediments. The ecologic model may be unable to simulate structurally complex systems with marshes, littoral zones, important sediment interactions, and diffuse inputs from the watershed, ground water, and the atmosphere.

7.3.5 Coniferous Forest Biome Stream Model

The stream model of McIntyre and Colby (1978) uses a modelling approach developed for the Coniferous Forest Biome. This model is a product of a number of years of research within the Coniferous Forest Biome and collaboration with researchers in other parts of the country. A hierarchical approach has been used to describe different aspects of general lotic ecosystems. References can be found in McIntyre et al. (1975), Overton (1975), and McIntyre and Colby (1978). A similar stream modelling program has been documented by Boling et al. (1975).

Objectives and Philosophy

The major purpose of the modelling program has been to develop and examine a general lotic ecosystem paradigm compatible with current concepts about lotic structure and behavior. A purpose of the modelling approach is to "increase understanding of behavior of fundamental biological processes in lotic ecosystems and to generate meaningful hypotheses related to lotic dynamics at relatively coarse resolution" (McIntyre and Colby 1978). Specific objectives include determining which levels of resolution are "necessary for adequate representation of environmental problems and management strategies" and establishing whether "stream processes are controlled by physical environment, food resources, predation, or behavioral adaptations of organisms."

Generality

Although this model has been calibrated for streams in the Pacific Northwest, it is thought to be applicable for any stream of orders 1 - 4 (defined by Cummins 1975). Benthic processes are represented in the model but water column processes important in large streams and rivers are not. Much of the information used in the model is obtained from the general literature.

Levels of Resolution

The theoretical aspects of the hierarchical paradigm (FLEX) and the modelling program have been developed and discussed in Overton (1972, 1975, 1977). Computer implementations of the FLEX paradigm are called FLEX2 and FLEX3 (White and Overton 1974).

The stream model has been characterized as having relatively coarse resolution, although several levels of resolution are developed within the model. Seven basic processes occur at the lowest or mechanistic level: periphyton dynamics, grazing, shredding, collecting, vertebrate predation, invertebrate predation, and detrital collection. These processes are aggregated into intermediate level processes: detritivory, herbivory, primary consumption, and predation. At the upper level are ecosystem processes, such as total production, which are aggregates of lower and intermediate level processes.

Model Structure

Stream processes are described by 14 state variables which represent biomass involved in the processes. Biomass is related to the processes by the "unit of capacity," defined as the rate of consumption per gram of biomass. State variables have been selected on the basis of functional groupings of organisms important in energy transfer within the streams (Cummins 1975). These functional groupings are not related closely to taxonomic categories and are called "quasispecies." These groupings are different from the "paraspecies" approach of Boling et al. (1975) which includes taxonomic considerations.

Nutrient interactions are not included in the model (McIntyre and Colby 1978) but are used as inputs from the environment as part of aquatic-terrestrial couplings. Detrital processes form an important submodel, which is consistent with the view of small streams as heterotrophic systems. Five categories of organic material with varying size, decomposability, and digestibility characteristics are used. There are fewer organic categories than in the Boling et al. (1975) model which has 32 categories.

Field data for stream discharge, channel depth, width, cross-sectional area, slope, current velocity, and suspended load are required for running the model. These hydrologic variables constrain the basic biotic, chemical, and physical processes. Temperature, photoperiod, and input of allochthonous inputs are important controls simulated by the model.

The model is hierarchically modular and allows for flexibility in modifying simulated processes. Conceptualization of the model is in discrete time with a basic time step of one day. One to six or more years are simulated during each run.

Systems Analysis and Simulation

A number of standard simulations have used data from the literature, from Oregon streams, and from laboratory and simulated stream experiments. Model validation was done by comparing calculated values with observed values. Various program modifications assessed model behavior. The model was run after one or more basic processes had been eliminated in order to examine the effects of process removal. Light inputs were changed to simulate stream behavior within different geographical regions or with different canopy covers. A perturbation analysis was done which simulated the effects of canopy removal from a forested stream. Results from these modified runs helped to generate new hypotheses about system behavior.

Assessment

The stream model of McIntire and Colby (1978) realistically simulates stream behavior and has served to give insight into ecological processes. The hierarchical approach for modelling aquatic ecosystems is unique and provides a valuable tool for ecosystem modelling and understanding ecosystem properties; the approach allows questions to be formulated and addressed at several levels of resolution. Effects of nutrient loading cannot be adequately simulated until a nutrient submodel is included. Water column processes need to be better developed before the model can simulate processes in large rivers and streams. This model should not be as capable of fine resolution prediction of detrital processes as the Boling et al. (1975) model which includes more detrital compartments.

7.3.6 Energy Circuit Language

The principle feature of a modelling approach developed by H. T. Odum is the energy circuit language which incorporates basic physical and chemical laws. This approach has been used for a number of models prepared at the Center for Wetlands at the University of Florida (Littlejohn 1973; Gayle 1975; Gilliland 1975; Lugo et al. 1976; Odum 1978). The fundamentals of the energy circuit language can be found in several places (H. T. Odum 1968, 1971, 1972, 1976).

Objectives and Philosophy

The philosophy behind the energy circuit language rests on several tenets: energy can be used as a common denominator for expressing ecosystem behavior, ecosystem dynamics can be expressed by simple physical and chemical laws, and it is possible to realistically and usefully simulate complex ecological systems using holistic or macroscopic properties. One major purpose is to have a comprehensive language which expresses the behavior of complex ecological or social systems.

Two sets of models will be examined here. Models for the evaluation of cypress domes in treatment of sewage have been developed by the Center for Wetlands (Odum 1978). The major objective of the cypress dome project is to determine the feasibility of using cypress domes or cypress swamps for management of wastewater. More specific objectives include simulation of possible effects of sewage application, fire, and harvest in cypress domes, and simulation of regional interactions with cypress domes. A second set of models deals with phosphorus management in Florida and more specifically with phosphorus management in the Peace River/Charlotte Harbor estuarine system (Gilliland 1975). The objectives were to evaluate phosphorus flows in Florida and to test effects of population growth and alternative effects of water and wastewater management on the estuarine system.

Generality

The modelling theory of H. T. Odum is general and capable of simulating a wide range of phenomena in ecological, economic, and social systems. Among systems modelled using the energy circuit language are wars (Odum 1968, 1972), marine ecosystems (Odum 1972), and tropical rain forests (Odum and Pigeon 1971). Because of their holistic and general nature, models built for one system can be applied to similar systems.

Levels of Resolution

When simulating an ecosystem using the energy circuit language, models at different levels of resolution are constructed. The cypress dome project uses a fine resolution phosphorus model which describes the role of aquatic vegetation, particularly duckweed, in phosphorus and nitrogen uptake and conceptualizes the effect of harvest and fire on cypress domes. Another model shows interrelationships of the cypress domes with the surrounding watershed. A third model describes competition of plants for nutrients within cypress domes. The Peace River/Charlotte harbor estuary project includes models at three levels of resolution. The coarsest resolution model examines phosphorus dynamics and storages for peninsular Florida. A second model describes the nutrient dynamics within the Peace River/Charlotte Harbor estuarine system. At fine resolution are process models describing nitrogen, phosphorus, and productivity relations in the mouth of Peace River.

Model Structure

Components of the energy circuit language can be translated directly to a differential equation which describes their behavior. Some components are modules consisting of several simpler components hooked together. Simple components behave linearly while modular components are nonlinear.

Interactions among nutrients are modelled with mass action laws which state that rates of reaction are determined by the product of concentrations.

involved. Converting nutrients to energy flows and measuring the interrelations between nutrients and energy flows can be difficult.

Many models are point models which describe properties and dynamics for an average area. Although energy circuit diagrams depict spatial relations within an ecosystem, as in the Peace River model, it is difficult to mathematically simulate spatial diversity on an analog computer.

Systems Analysis and Simulation

Simulations using energy circuit language are centered on the analog computer, because of the language's close relationship to electrical network diagrams. Use is made also of digital computers and CSMP, DYNAMO, and FORTRAN.

Simulation on the analog computer is useful for displaying the behavior of small ecosystem models. Dynamics can be expressed visually, and there is immediate feedback between observer manipulation and resulting behavior. A problem with the analog computer is determining easily the realism of value combinations because of the need to scale values (Wiegert 1975a).

Usefulness of the energy circuit language is restricted to models of small size. As Odum points out, the intuitive value gained is greatest for small models. The diagrams have inherent limitations in size; information gained by examining a diagram of a system decreases after a threshold of complexity is exceeded. The usefulness of the analog computer decreases as models become large because computer capacity is exceeded. The mathematical formulations become unmanageable because of the combination of nonlinearities; certain energy circuit models have five to eight state variables multiplied together (Odum et al. 1974; Gayle 1975).

Assessment

One of the energy circuit language's useful features is its ability to communicate a macroscopic perspective to ecosystem and social managers. The models are relatively quick to develop and run, in contrast to other models which often require many man-years to build and calibrate. Ecologists and modellers need to evaluate whether or not macroscopic ecosystem behavior obeys closely laws which describe simple, ideal physico-chemical systems. Another point which should be evaluated is the usefulness of looking at an ecosystem completely from an energy point of view. Although ecosystems and their processes can be described in terms of energy, it may not be the most appropriate means for addressing many questions. Ecosystems are multivariate systems, and their behavior can be described by various forms of matter and energy simultaneously.

7.3.7 Lake Texoma Cove Model

The Lake Texoma Cove model is a mathematical description of ecological relationships occurring within a cove of a Texas-Oklahoma reservoir. The model was developed as a teaching exercise for a group of postdoctoral researchers under the direction of B. C. Patten. A detailed description of the model and simulations is presented in Patten et al. (1975).

Objectives and Philosophy

Several objectives were identified by modellers at Lake Texoma: to characterize the unperturbed biomass dynamics of the cove ecosystem, to understand the cove as an ecological unit, to examine the response to small, realistic perturbations, and to explore the usefulness of linear systems analysis. The model was intended to demonstrate the usefulness of linear-donor controlled modelling for ecosystem analysis. Discussion in the Lake Texoma paper outlines basic features of the linear-donor controlled modelling philosophy which also is discussed in Waide et al. 1974; Patten 1975b; Patten et al. 1975; and Webster et al. 1975. However, at least 35 percent of the interactions in the model as described in Patten et al. (1975) are nonlinear and a significant number are recipient or donor-recipient controlled. This discrepancy compromises the model and makes it difficult to evaluate with respect to the last objective. Recently, the nonlinearities have been linearized and simulations run at the University of Georgia (C. I. Liff, personal communication); however, these corrections do not yet appear in the literature.

Generality

The Lake Texoma Cove model simulates the behavior of a cove in a southwestern reservoir, but the holistic linear philosophy makes it possible to simulate other aquatic ecosystems with a minimum of recalibration and restructuring. Much of the model is general, representing basic processes occurring in all aquatic ecosystems. Many interactions and coefficient values were taken from the general ecological literature and are not specific to Lake Texoma.

Level of Resolution

The Lake Texoma Cove model is a fine resolution model with 33 storage compartments representing biotic and chemical components. The model is run for periods of one to five years, using a time step of half-a-day, and output is printed at weekly intervals.

Model Structure

The 33 compartments are aggregates of more than 200 compartments initially identified in workshops. There are not special compartments which reflect regional considerations. The compartments were divided into primary producer, zooplankton, decomposer, and vertebrate submodels. Compartments and their dynamics are described by mass relations. Carbon, hydrogen, oxygen, phosphorus, and nitrogen are related to compartment mass by stoichiometric ratios. Potential nitrogen, phosphorus, and carbon limitations are included in the formulation of nutrient dynamics. Nitrogen and phosphorus are considered to be limiting in the cove, but it is assumed that carbon is never limiting.

Seasonal dynamics of compartments are expressed by making some coefficients depend on time varying functions (sine waves) which represent temperature and light. Real data can be substituted for these simple functions. Many interactions are dependent on the initial state of the compartments and are independent of them thereafter.

Nonlinearities occur in the descriptions of vertebrate feeding, nutrient uptake by plants, zooplankton feeding, and phosphorus relations with organic matter. As noted earlier, these nonlinearities have recently been removed from the model, although this correction does not yet appear in the literature.

Driving functions include wind, atmospheric invasion of gases, precipitation, light, temperature, and turbidity. Physical processes such as circulation, turbidity changes, light extinction, and water level fluctuations are also modelled. The effect of water level change on biota was modelled by a subroutine which simulated habitat changes. The cove is regarded to be a well-mixed system, and vertical stratification is not included. Because of the shallow depth, sediment relations are important but are inadequately modelled as explained in the documentation of the model.

No attempt was made to model the watershed surrounding the Texoma Cove. Simple time-varying inputs from the land are used. These inputs are based on precipitation and vegetation cover and represent dissolved and particulate organic matter, phosphorus, nitrogen, and carbon.

Systems Analysis and Simulation

Because little dynamic information about the cove was available, no formal validation procedure was used for the simulated behavior. The validity of model behavior was assessed in terms of reasonableness of expected behavior. Several perturbation trials were done, and the results were judged to be reasonable by the authors. Recently the behavior of the linearized model was compared with the behavior of the nonlinear model described in Patten et al. 1975. Unperturbed behavior of the linear model was similar to the unperturbed behavior of the nonlinear model.

Assessment

Linear modelling provides a quick way to describe and organize the information about ecosystems. Useful insight can be gained by examining the structure and behavior of linear ecosystem models (Patten 1972b; Waide et al. 1974; Webster et al. 1975). The use of linear models has been defended because of the well-developed engineering techniques which can be applied to them; however, the restrictions and assumptions behind linear formulations must be well understood before results from these techniques can be interpreted. Given the success of nonlinear models (Wiegert 1975b; Chen and Orlob 1975; Park et al. 1978), there appears to be no reason to restrict modelling efforts to linear formulations. Linear models will probably not predict accurately quantitative results of large perturbations to ecosystems but will describe qualitative ecological behavior. Many ecologists do not regard linear-donor controlled formulations as being realistic for describing many ecological processes (Wiegert 1975a; Bledsoe 1976). Large linear models can be constructed, calibrated, and solved efficiently.

7.4 SYSTEMS ANALYSIS TECHNIQUES

A number of systems analysis techniques have been presented in the literature for examining ecosystem models. Systems analysis techniques can be used to generate hypotheses about ecosystem structure and behavior and can help validate or invalidate a model as a statement about ecosystem structure and behavior. Among systems analysis techniques applied to ecosystem models are model aggregation or condensation, simulation, perturbation analysis, sensitivity analysis, flow analysis, stability analysis, and network analysis.

7.4.1 Aggregation

Aggregation involves combining components and processes which have certain taxonomic, structural, or functional characteristics in common; disaggregation involves breaking components up into constituent subcomponents. In mathematics "decomposition" is used to describe the partitioning of a set into subsets (Simon 1973). Because "decomposition" already has a well defined meaning in ecology, use of this word is confusing and inhibits communication between theoreticians and ecologists. Disaggregation has been used equivalently to decomposition in the sense of partitioning a set into subsets (Park et al. 1978). Model condensation has been used equivalently to aggregation (Wiegert 1975b; Halfon and Reggiani 1978).

Aggregation is a useful modelling tool and one that can be used to impart a feeling about ecosystem structure and behavior (Odum 1972; Zeigler 1974, 1976; Wiegert 1975b; Overton 1977; Halfon and Reggiani 1978; McIntyre and Colby 1978). In the modelling approaches of Patten (1975a) and Odum (1972, 1976), the initial model may be a conceptual model comprising a large number of components and interactions known to be important in the ecosystem of interest. This large set of components and interactions then is aggregated into smaller sets which are mathematically and conceptually manageable. The exercise of deciding which components, interactions, and processes are aggregated is important in imparting the macroscopic perspective discussed by Odum (1976).

There may be no best way to aggregate a large set of components which make up the conceptual description of an aquatic ecosystem. Although taxonomic considerations have been used to define components, they are not always useful. Different development stages of a species may have different functions or spatial distributions (Cummins 1973), making it difficult to aggregate some components along taxonomic lines. Components may be aggregated according to both functional and taxonomic characteristics (Boling et al. 1975; McIntyre and Colgy 1978). A good strategy for defining components is to aggregate or disaggregate them in a manner consistent with operational techniques; it is often easier to measure composite properties of a large group of organisms rather than properties of individual organisms or populations. Another useful way to aggregate components is according to their spatial distribution in aquatic ecosystems. Operational techniques often are compatible with spatial distribution of ecosystem properties.

7.4.2 Simulation and Perturbation Analyses

The most basic systems analysis technique is simulation which involves solving the equations which describe behavior of the system being modelled. Solution of the simple water quality models results in the state of an ecosystem at a particular point in time, usually at the end of a year. Solution of comprehensive ecological models results in trajectories of ecosystem properties through time.

A simple modification of simulation is to change the values of coefficients and variables of the model and to examine resultant behavior. The analog computer is ideal for examining the behavior of a simple differential equation model (Patten 1972a). Although solutions to equations can be displayed visually immediately, the analog computer is restricted to fairly small models. Digital simulation is useful for large models and can be used with both differential, difference, and stochastic equations.

Perturbation analysis is a simple sensitivity technique in which coefficient or state variable values are changed. Perturbations are relevant to impact analyses because they can represent nutrient or sediment inputs. Although some perturbations have no real meaning, they may be used to analyze model behavior. Engineering techniques make use of standard perturbations which can be analyzed formally; the use of the pulse function and the unit step input function are described in Zadeh and Desoer (1963) and Waide and Webster (1976).

7.4.3 Sensitivity Analyses

Because components of a model are constrained by one another in both direct and indirect fashion, it often is difficult to ascribe a model's behavior to a particular coefficient. Sensitivity analyses examine model behavior in terms of changes in coefficient values. The simplest is a perturbation analysis which involves separate modification of each coefficient and subsequent solving of the modified model. A more sophisticated technique has been used by the Eastern Deciduous Forest Biome modelling program; perturbations of various magnitudes are generated randomly in each of a number of runs and the resulting runs are evaluated. This type of sensitivity analysis is time consuming and expensive but works on a broad range of models. More sophisticated techniques examine all coefficient and state variables simultaneously (Tomovic 1963; Tomovic and Vukobratovic 1972). Sensitivity coefficients for a variable describe the relative and absolute effects of small changes in coefficient values. This technique can identify the most sensitive parts of a model; i.e., the variables which most influence model behavior. The analysis demonstrates the effect of measurement error on model variables and assesses parts of a model which require most attention. Extrapolations from sensitivity analyses to real ecosystems should be done with reservation and need to be tested. Discussions of sensitivity analyses and their relationship to ecology are found in Patten (1969), Gallopin (1971) Kowal (1971), Brylinsky (1972), Parker (1975a), Waide and Webster (1976), Astor et al. (1976), and Park et al. (1978).

7.4.4 Network Analysis

Some of the simplest and most straightforward of the systems analysis techniques are network analyses. These analyses are based on the idea that components in an ecosystem dependency network are related both directly and indirectly (Levins 1975; Patten et al. 1976; and Land and Levins 1977). The dependency structure of a system can be described by graphical and matrix techniques. Graphic techniques are pictorial and make use of compartments which represent storages and arrows between compartments which represent interactions.

A simple compartment model is shown in graphical form in Fig. 7.1. A graph can be simply transformed to matrix notation. A matrix representation of the graph in Fig. 7.1 is shown in Fig. 7.2. Each row and column represents a compartment in the graph. Entries in the matrix represent interactions (arrows) between compartments. Entry (i,j) represents the interaction from compartment $\underline{j}$ to compartment $\underline{i}$ in the graph. Matrix $\underline{A}$ is called the adjacency matrix of the model and shows the position of all direct paths in the graph. When matrix A is multiplied by itself, the resulting product shows the position of all two length paths in the graph; $\underline{A}^3$ represents all the three length paths and so on. Symbols can be used in place of numbers in the matrix and can trace impacts through an ecosystem network. An asterisk has been used in matrix $\underline{A}$ to indicate the direct impact of organic pollution on bacteria. In $\underline{A}^2$ the position of asterisks shows components (Protozoa, *Diapatomus*) influenced by two length paths which have relayed the direct impact on bacteria. In $\underline{A}^3$, $\underline{A}^4$, and $\underline{A}^5$ one can see by the position of the asterisks which components (*Cyclops*, *Asplanchna*, fish, organic material, and outflow) are affected indirectly by direct impact on bacteria. Dissipation of impact occurs further from direct impact; the impact becomes diluted by the dependency network (Hill 1979). These techniques can be used to show the positions of direct and indirect impact in ecosystems and to trace through an ecosystem network to see what components will be affected by an impact.

This network analysis is related to several techniques. Network analyses have been done by Levins (1975) and Lane and Levins (1977) and indicate whether or not interactions have a positive or negative influence on ecosystem processes. Network analyses have been used to quantify structural characteristics of network (Hill and Durham 1978; Hill 1979). Relationships between flow analyses (Hannon 1973; Finn 1976a, 1977) and network analyses are discussed in Patten et al. 1976; Barber et al. 1978. Markov chain analyses of Barber (1978a, 1978b) also are related to network and flow analyses.

7.4.5 Stability Analyses

Stability has received a great deal of attention in ecosystem ecology and modelling. Stability is related to the persistence of ecosystems and ecosystem models through time (Margalef 1968; Lewontin 1969; May 1971, 1974, 1976). Implicit in ecosystem stability is the existence of a normal range of variability within which characteristic properties of an unperturbed ecosystem remain for an extended period of time. Perturbations to ecosystems tend to drive the observed values of these properties outside their normal range. Stability implies the tendency of the perturbed properties to remain within

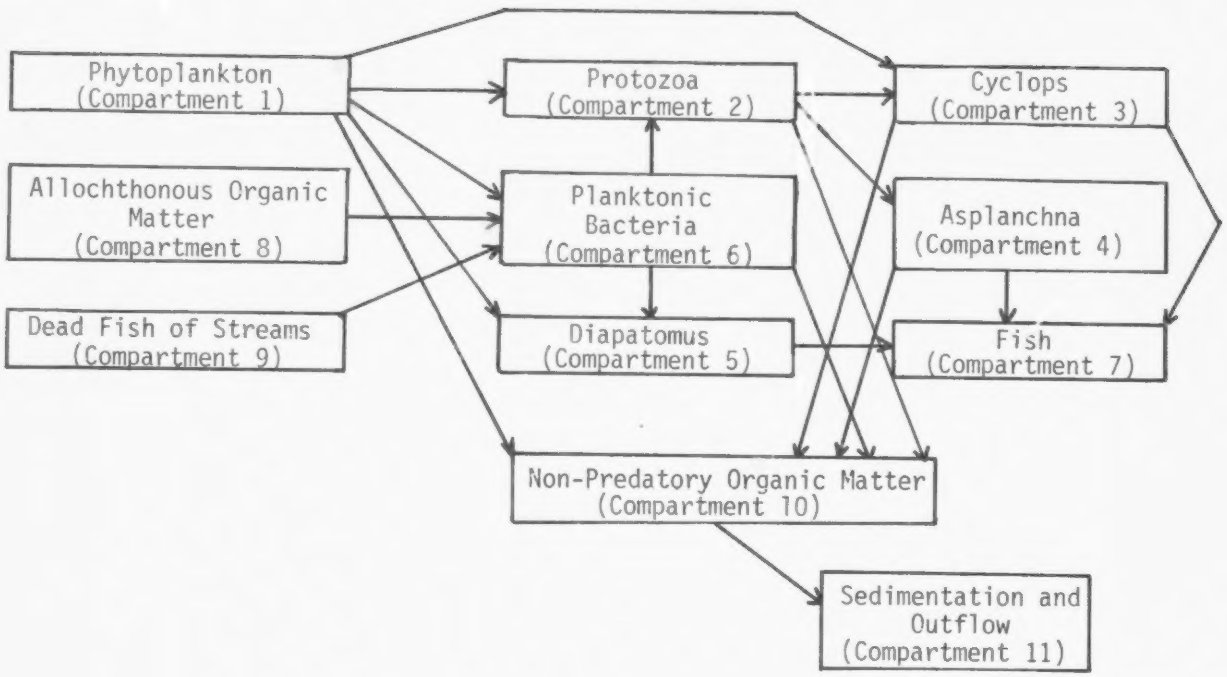
Phytoplankton (Compartment 1)
Allochthonous Organic Matter (Compartment 8)
Dead Fish of Streams (Compartment 9)
Protozoa (Compartment 2)
Planktonic Bacteria (Compartment 6)
Diapatomus (Compartment 5)
Cyclops (Compartment 3)
Asplanchna (Compartment 4)
Fish (Compartment 7)
Non-Predatory Organic Matter (Compartment 10)
Sedimentation and Outflow (Compartment 11)

Fig. 7.1. Energy model of pelagic region of cove. (From Sorokin and Paveljeva 1972.)

A: First Order Adjacency Matrix showing direct effects (1 path length)

	1	2	3	4	5	6	7	8	9	10	11
1											
2	1					1					
3	1	1									
4		1									
5	1					1					
6	1							*	1	1	
7			1	1	1						
8											
9											
10	1	1	1	1			1				
11										1	

A^2: Second Order Adjacency Matrix (2 path-lengths)

	1	2	3	4	5	6	7	8	9	10	11
1											
2	1							*	1		
3	1					1					
4	1					1					
5	1							*	1		
6	1	1	1	1		1					
7	1	1				1					
8											
9											
10	1	1	1	1	1	1					
11	1	1	1	1			1				

A^3: Third Order (3 path-lengths)

	1	2	3	4	5	6	7	8	9	10	11
1											
2	1	1	1	1		1					
3	1							*	1		
4	1							*	1		
5	1	1	1	1			1	*	1		
6											
7	1					1		*	1		
8											
9											
10	1	1				1		*	1		
11	1	1	1	1	1	1					

A^4: Fourth Order (4 path-lengths)

	1	2	3	4	5	6	7	8	9	10	11
1											
2											
3	1	1	1	1		1					
4	1	1	1	1		1					
5											
6	1	1				1		*	1		
7	1	1	1	1			1	*	1		
8											
9											
10	1	1	1	1		1		*	1		
11	1	1				1		*	1		

A^5: Fifth Order (5 path-lengths)

	1	2	3	4	5	6	7	8	9	10	11
1											
2	1	1				1		*	1		
3											
4											
5	1	1				1		*	1		
6	1	1	1	1		1		*	1		
7	1	1	1	1		1					
8											
9											
10	1	1	1	1		1	1	*	1		
11	1	1	1	1		1		*	1		

$\sum_{i=1}^{5} A^i$: Sum (1-5 path-lengths)

	1	2	3	4	5	6	7	8	9	10	11
1											
2	1	1				1		*	1		
3	1	1				1		*	1		
4	1	1				1		*	1		
5	1	1				1		*	1		
6	1	1	1	1				*	1		
7	1	1	1	1	1	1			1		
8											
9											
10	1	1	1	1	1	1	1	*	1		
11	1	1	1	1	1	1	1	*	1	1	

Fig. 7.2. Products of adjacency matrices with asterisks to show position of direct and indirect impact.

their normal range or to return to it if moved outside. Resistance is the component of stability related to the magnitude of the perturbation required to drive properties outside their unperturbed range. Resilience is the component of stability related to the time required for perturbed properties to return to the unperturbed range.

Stability in mathematical models is analogous to stability in ecosystems. In a stable model properties return to their normal trajectories after perturbation. Model resistance and resilience have analogous definitions to ecosystem resistance and resilience (Long 1974; Waide and Webster 1976; Webster et al. 1975). Techniques for assessing the stability of models include qualitative assessment of model behavior, quantitative deviation from normal behavior, existence of negative eigenvalues, and frequency response analyses. Deviation from normal trajectories can be determined and assessed visually and mathematically. Techniques such as existence of negative eigenvalues and frequency response analyses have been restricted to small, linearized ecosystem models (Bledsoe 1976). Further discussion of stability analyses are found in MacArthur (1955); Tomavic (1963); Patten and Witkamp (1967); Odum (1969); Watt (1969); Thom (1972); Parker (1973, 1975a, 1975b); and Zalucki (1978),

Stability analysis of models has implications for impact assessment in aquatic ecosystems. Formal stability analysis has been applied to a model of Lake Kootenay, British Columbia, in order to assess ecosystem stability at various points in time (Parker 1975a, 1975b). The model, documented in Parker (1973, 1974), describes the dynamics of algae, crustacean zooplankton, phosphate, nitrate, and ammonium in an ecosystem receiving effluent from a fertilizer plant. Using negative eigenvalue techniques (Parker 1975a) and sensitivity analyses (Parker 1975b), the model was shown to be "extremely" stable.

7.4.6 Frequency Response Analyses

Many natural inputs to ecosystems are periodic. Some, such as light and temperature, are approximately sinusoidal and can be characterized by frequency and amplitude of their oscillations. Periodic inputs are transmitted through the dependency network of an ecosystem model, and because of constraints arising from the coupling between components, the model will modify the amplitude and frequency of inputs. The degree to which periodic inputs are modified and reflected in model output can be examined by linear engineering analysis. Amplitude and frequency that have been altered by a model reflect the structure and time constants of the model (DiStefano et al. 1967; Child and Shugart 1972; Waide and Webster 1976).

The damping factor and natural frequency are two parameters derived from frequency response analysis. According to Child and Shugart (1972), Waide et al. (1974), Waide and Webster (1976), and Harwell et al. (1977), the damping factor and natural frequency are related to the resilience and resistance of mathematical models. It would be useful for impact analysis to be able to quantify the resistance and resilience of an ecosystem to perturbation of phosphorus, nitrogen, carbon, and sediments.

7.4.7 Flow Analyses

In material and energy models compartments represent storage, and the interactions represent movement of materials or energy between compartments. In order to assess the magnitude of indirect flows of a model, flow analysis techniques have been developed. Flow analysis can examine how much an outflow is influenced by each of the compartments and inputs in the model. Flow analyses used in ecology are derived from input/output analyses for economic systems derived by Leontief 1966 (Hannon 1973; Finn 1976a; Patten et al. 1976). Input/output analyses indicate which inputs or compartments can be adjusted to give a particular output or set of outputs. Theoretically, flow analyses tell researchers how to modify inputs to real systems in order to adjust storages and outputs in real systems. This ability would be useful for pollution management of aquatic ecosystems. With flow analyses and a good model, the effect of a change of phosphorus input on phosphorus storage and phosphorus output can be determined.

Indices which reflect the degree of material cycling can be determined for ecosystem models (Finn 1976a, 1976b, 1977). These indices have been used recently to compare structural differences among four lake models (Richey et al. 1978). Flow analyses can be interpreted easily only for relatively simple systems which are at or near steady state. A related analysis is the Markov chain analysis used to trace the paths of material or energy through a model network (Barber 1978a, 1978b; Barber et al. 1978). This analysis is compatible with statistical techniques, and confidence intervals can be placed on a number of derived quantities.

7.4.8 Validation

Validation is the process by which model behavior is related to the real world. According to Webster's Collegiate Dictionary (1976), "to validate" means "to make valid; substantiate; confirm." Hypothesis testing in terms of the scientific method may be regarded as a specific category of validation. The process of validating ecosystem models has been discussed in a number of papers (Innis 1975; Wiegert 1975a; Caswell 1976; Levins 1966; Mankin et al. 1977).

The validity of a model can be assessed in several ways depending on the objectives of the model, accuracy and precision of model output, reasonableness of model output in terms of observations and experimentation, and reasonableness of interaction patterns and mathematical formulations in terms of ecological theory. These three ways of validation are not related necessarily to one another, as pointed out by Levins (1966). For example, an unreasonable model may give accurate predictions and a reasonable model may give inaccurate predictions (Caswell 1976). The iterative operation of the scientific method should draw the above features of validation together (Becht 1974), i.e., realistic models should become increasingly more reasonable, precise, and accurate.

Caswell (1976) has argued that validation of ecosystem models be done by disproving hypotheses derived from models rather than testing the model itself. Levins (1966) asserts that ecosystem models cannot be hypotheses because experiments with ecosystems cannot be done. However, both terrestrial and aquatic ecosystem experiments have been done (Likens and Bormann 1972; Swank and Douglas 1975). Examining a large population of lakes and rivers subject to a variety of natural and man-made inputs can be equivalent in some respects to laboratory experimentation. Model structure is addressable as scientific hypotheses in terms of such experimental results. Identification of the relationships occurring in real ecosystems is a problem at the basis of ecosystem modelling and one that is addressable by formal statistical techniques (Halfon 1975a, 1975b).

Because an infinite number of models will fit any particular data set equally well (Bunge 1959; Popper 1959), most ecological modellers have used qualitative "goodness-of-fit" criteria for validating models. Models are judged as to whether they behave reasonably well or similar to behavior expected in ecological systems. A model often is calibrated and compared to a data set that was not used to construct the model. Another technique is to use the data from one year to construct the model and another year's data to validate it.

Caswell (1976) suggested that model validation proceed through testing submodels via rigorous experimentation. Attention also must be paid to the manner in which the submodels are connected together; i.e., to the upper level hypotheses which constrain the interconnected submodels. Formulating and testing whole system constraints and behavior is as important as testing submodel and component behaviors.

7.5 SUMMARY

Mathematical models which describe observed variation in aquatic ecosystems have become increasingly sophisticated in the last few years. Each model describes a response surface and is capable of predicting response due to changes in system inputs and controls. Because many components, processes, and mechanisms are basic to all lakes and rivers, ecosystem models are relatively general but require specific information on inputs and chemical and physical parameters which control individual ecosystem behavior. Coarse resolution models generally do not deal with dynamic properties and predict only gross effects of nutrient loading. Although they have been used for both lakes and rivers, coarse resolution models do not work well in spatially diverse systems. Fine resolution models describe the dynamic variation of several observed properties. Most fine resolution ecological models have been built for lakes rather than for streams, marshes, or swamps. The MS. CLEANER model of the Eastern Deciduous Forest Biome program represents the state-of-the-art in fine resolution lake modelling and can answer questions about nutrient enrichment, thermal pollution, siltation, impoundment, and fish removal (Park et al. 1978). MS. CLEANER is complex and expensive to run in its entirety; however, because MS. CLEANER is modular, only parts of the model are required to answer questions about aquatic ecosystems. Approaches such as Odum's (1972, 1976) and Patten's (1975a) may be better able to deal with behavior of complex ecosystems. Most fine resolution lake models are capable of dealing with systems which are partitioned into a few well-mixed sections; however, they will not describe slow-moving systems such as marshes, swamps, and littoral regions. Recent models of swamp and marsh systems (Odum 1978; Kadlec 1978) have begun to deal with these poorly mixed aquatic ecosystems. Fine resolution stream models (Boling et al. 1975; McIntyre and Colby 1978) predict behavior of stream components and processes when driven by allochthonous carbon sources. These stream models do not yet include nutrients.

A major problem still facing aquatic ecosystem modelling is the inability to adequately characterize inputs. Inputs from atmosphere, watershed, tributaries, and ground water drive aquatic ecosystems through time, the dynamic behavior of ecosystem conponents is entrained largely by the temporal variation of inputs (Patten 1978). Many inputs are difficult to measure because they initiate from nonpoint sources and vary with time. Watershed, land use, and meteorological characteristics establish the input regime of aquatic ecosystems.

Systems analysis techniques can play important roles in impact assessment. Perturbation analysis of models, for example, can be used to describe behavior of ecosystems to which pollutants have been introduced. Sensitivity analyses can identify parts of an ecosystem most sensitive to impact, indicate what information should be sought, and assess the effect of measurement error. Stability analyses can evaluate how much, and how quickly a system should respond to impact and then return to normal behavior. Flow analyses can suggest how nutrient and sediment inputs to ecosystems can be adjusted to give desired behavior and how much internal cycling contributes to system behavior. Certain systems analysis techniques are restricted to a small set of simple models. Simulation and perturbation trials can be used on most models and probably can provide as much information as sophisticated sensitivity techniques. However, it is possible to make models too complicated and unstable to simulate. A number of sophisticated systems analysis techniques are derived from engineering theory and are best suited for simple linear or linearized models. The claim that they provide interesting and useful results applicable to ecosystems should not be taken for granted, but the assumptions behind them should be examined.

Mathematical models are statements about ecosystem behavior and demonstrate properties analogous to ecosystem behavior. Models and systems analysis techniques must be incorporated into the normal operation of the scientific method; they must be validated, corroborated, and used to generate other statements about ecosystems. Ultimately the best criteria for evaluating models are success and acceptance by users. If a model predicts behavior well for a number of systems under various conditions, then it will be considered a good model. As ecosystem modelling evolves, "natural selection" of models will occur, and many problems found in earlier models will be resolved.

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CHAPTER 8

SUMMARY OF ORGANIZING CONCEPTS

In the preceding chapters we have explored an organizational scheme to evaluate the impact of nutrients and sediment on the biota of the nation's waterways. To carry out this objective we utilized the ecosystem concept which states that systems of biotic and abiotic units interact to form coherent systems that have predictable properties. We next adopted the concept that the great variety of ecosystems that are recognized at different scales of complexity, over spatial scales, and at different times can be organized into a hierarchy. The hierarchy we developed combines large geographic units with more restricted biological units.

We find that the hierarchy is useful for organizing the work of the study, since aquatic systems are immensely varied; to generalize to all lakes or rivers within geographic regions results in loss of much of the biotic character of the system. At the upper levels of the hierarchy the physiocochemical factors, especially those related to the land, direct system behavior; at lower levels biotic roles become more important.

Thus, we have identified a resolution problem related to water management. Management of water quality, from a physico-chemical point of view, can be carried out at coarse levels of resolution, if one is willing to accept changes in biota. Management of biota, on the other hand, is carried out at a fine level of resolution, and regulations must be geographically specific. Quite clearly, regulations and programs directed to the same resource (aquatic systems) can conflict by focusing on different levels of resolution.

Since the project objective specified biota as the target of interest, we have explored in detail (in Chapter 6) those levels of the hierarchy where the biotic component is dominant or very significant. These include communities, species populations, and individuals. We conclude that there are a great variety of structural and functional attributes of biota which could be used to predict responses of biota to nutrient and sediment impact. We are not able to judge what are the best criteria, however. The best criteria should reveal a great deal of information about the biotic unit, be general in reference to many types of similar biotic units, be conservative, and be responsive to the specific impact of concern. Various authors have argued that many different criteria fit this standard.

We feel that the solution to this problem is the adoption of a dynamic approach to system analysis and management. If we assume that aquatic systems are not static, but rather are dynamically changing, then our concern is with the direction and rate of change. Our focus shifts from the structure to the function of systems, recognizing that structure will shift to maintain functional attributes within limits of stability. This point of view is not congenial to those who wish to hold system structure (especially the species structure) fixed in time. If that is the goal, then the management alternatives are quite different. We believe that these two points of view are contradictory, and if both points of view are pursued then conflict must occur.

Nevertheless, the trend reflected in the literature stresses biota and requires a structural view in part. Therefore, we seek vulnerable systems, components, and populations. Vulnerability is expressed by a biotic response to changes in nutrient or sediment levels, which often can be described by response curves. These curves can provide information required to model responses of biota under the complex interactions in ecosystems. Of course, it is usually difficult to carry out experiments on biotic response in the field. Not only are there mechanical problems, but the uncontrollable interacting variables necessitate large sample sizes and complex statistical procedures. Thus, response studies are usually carried out in the laboratory, and it is difficult to determine if the data under controlled conditions can be extrapolated to the field.

Because of the twin problems of scale resolution and a static-dynamic analysis, we have constructed models of the freshwater systems at two levels of resolution--a fine level and a coarse level. Coarse level modelling approaches provide a relatively quick and inexpensive prediction of system behavior, while fine level approaches incorporate biotic interactions and temporal variations. Also, the problem of impact prediction depends upon the accuracy or the confidence required in the prediction. Validation seems not to be developed sufficiently to specify the predictive confidence resulting from specified types of models. However, confidence increases as the resolution increases. But the degree of resolution is clearly limited both by the computing machinery and our ability to collect, reduce, and analyze the data required for a fine resolution. Fine level models have been developed for specific system types, but it is not apparent now how well any of the coarse level models can be applied to many different systems. This comparison would provide us with a way to judge which model to use in assessment of impact. However, as far as we know, a comparative study of this type has not been done.

Summarizing, the introductory sections of this report have utilized concepts that allow integration of the physical, chemical, and biological attributes of freshwater systems and that allow organization of the different types of waters at all levels of the hierarchy. We have found a variety of characteristics of biota and systems that could be used to describe biotic response to nutrient and sediment impacts depending on the hierarchical level considered. And, we have explored some modelling approaches for studying system dynamics and response. We also have uncovered several conceptual and methodological problems that mitigate against achieving the goal of integrated water management across the nation.

In the next section of the report we examine data on sediment and nutrient impacts on biota and judge if these data are sufficient or adequate for prediction. Chapters 9 and 10 analyze information at the lower levels of the hierarchy since most research has been conducted using specific organisms, communities, or water bodies. In the final chapter, Chapter 11, we show how the hierarchical scheme may be utilized to evaluate the sediment and nutrient impacts identified and we provide an analysis of our results in this hierarchical context.

CHAPTER 9

IMPACTS OF SEDIMENT ON BIOTA IN SURFACE WATERS

9.1 INTRODUCTION

The impact of sediment movement and deposition on aquatic biota in surface waters of the United States is reviewed and evaluated in this chapter. The review is primarily concerned with the effect of sediment on biota; the role of sediment as a carrier of nutrients will be treated in Chapter 10. Heavy metals and pesticides are also associated with sediments and may be detrimental to organisms in certain aquatic systems. The effects of these compounds are reviewed by the Environmental Protection Agency (EPA)(1976) and Kemp et al. (1973) and are not considered in this study.

9.1.1 Sediment Characteristics

The term "sediment" refers to any particulate material, transported from its site of origin by air, water, or ice, which is in suspension or has come to rest on the earth's surface (Trowbridge 1962). In terms of biological effects, sand, silt, and clay particles are of interest because they are readily suspended and transported by water.

Most sediment may be assigned to one of two broad categories:

1. Organic material in varying states of decomposition, ranging in size from colloidal particles to large detrital particles, and
2. Inorganic material ranging in size from colloidal particles through silts and sands to large boulders.

In practice it is difficult to completely separate organic and inorganic fractions of natural sediments, due to the reactivity of organic and inorganic colloids which results in the adsorption of organic colloidal compounds on solid surfaces (Grim 1968; Jenne 1968; Malcolm and Kennedy 1970; Greenland 1971; Schnitzer and Kahn 1972).

Sediment also may be classified by particle size. The size of sediment particles affects sediment transport and reactive surface area and influences the distribution of biota (Cummins 1975). A suggested terminology for particle size analysis of sediment was developed by the Subcommittee of Sediment Terminology of the American Geophysical Union and is widely used in the United States (see Gottschalk 1964). This classification scheme is based on particle size only, with no reference to the composition of the material in question.

Sediment is transported in the following two forms:

1. Suspended load - particles maintained in the water column by turbulence and carried with the flow of water; and
2. Bed load - particles resting on the streambed and pushed or rolled along by the flow of water.

Suspended load and bed load are functional descriptions used to distinguish two different modes of transport which follow different physical laws. Suspended load, composed primarily of silts and clays, is usually limited by the rate of supply from the watershed. Bed load is composed of larger particles, such as sand and gravel, which are not as easily maintained in the water column by turbulence. Movement of bed material is limited by the transporting ability of the channel, that is, by the shear stress applied to the bed by moving water. A given particle may move in either mode, depending upon the conditions. Sand, for instance, may move as suspended material at high water velocities associated with a steep gradient or high discharge. During periods of low flow or slower water velocities associated with gentle gradients, sand may move primarily as bed load (Chow 1964; Leopold et al. 1964; Gregory and Walling 1973). Passega (1957, 1964) distinguishes several forms of sediment movement representing a continuum between bed load and suspended load, including rolling, bottom suspension, graded suspension, uniform suspension, and pelagic suspension. Methods for distinguishing these sediment fractions are available (Passega 1964; Friedman 1967; Royse 1968), but the ecological significance of the various fractions is unknown.

9.1.2 Measurement of Sediment Transport

Measurements of transported bed load and suspended load often show large variations in time and space. These variations result from differences in channel geometry, sediment supply, and discharge. As a result, estimates of the total sediment yield are statistically accurate only if sampling is sufficient to detect periods of fluctuation (Einstein 1964; Piest 1965). Assessment of sediment yields rely either upon estimates of the total sediment load deposited within a reservoir or upon measurement of suspended sediment concentrations and estimates of bed load over a range of flow conditions. Bed load often is assumed to be 5 to 10 percent of the suspended load by weight (Wark and Keller 1963; Gregory and Walling 1973). For a detailed treatment of sediment sampling see Chow (1964), Einstein (1964), Guy (1969, 1970), Guy and Norman (1970), Porterfield (1972), Riggs (1973), and Gregory and Walling (1973).

The amount of sediment transported by a channel also may be estimated from theoretical consideration of the properties of the sediment and the potential of the channel to transport the imposed sediment load. These methods of sediment load estimation are based on equilibrium conditions which do not exist in an aggrading or degrading channel (Einstein 1964). Since the ability of a channel to transport material as suspended load often exceeds the rate of supply, theoretical simulations also must consider conditions within the watershed which affect the supply of sediment (Gregory and Walling 1973).

Biologically oriented studies often estimate suspended sediment concentrations by measuring the turbidity produced by sediment. Turbidity is an optical property of water causing light to be scattered and adsorbed rather than transmitted in a straight line. The amount of light scattered is a function of size, shape, and refractive index of the particles present, but has little direct relationship to concentration and specific gravity of the suspended material (American Public Health Association 1975). Turbidity is measured using a turbidimeter or a nephelometer both of which measure the intensity of light scattered at some angle to the incident light. An alternative method measures the length of the light path through a suspension which causes the image of a standard candle flame to disappear (Jackson candle turbidimeter). There is no direct relationship between Jackson candle turbidity and the intensity of light scattered at 90° (American Public Health Association 1975). A number of turbidity standards and units are used, including:

1. Formazin - reported as Formazin Turbidity Units or FTU.
2. SiO_2 - reported as ppm SiO_2.
3. Manufactured standards may be reported as Nephelometer Turbidity Units; Jackson Turbidity Units (JTU); or any of the preceding units.

The definitions of turbidity, units of measurement, and a comparison of the results and principles of measurement of a variety of turbidity meters have been reviewed by Duchrow and Everhart (1971) and McCluney (1975).

Suspended solids are determined by a gravimetric procedure. Generally, tared filters are used to filter a known volume of water. The filters are then dried to a constant weight and the amount of solids present reported in milligrams per liter (American Public Health Association).

9.1.3 Modifiers of Sediment Impact

Evaluating the effect of sediment on aquatic biota is confounded by variations in the physical and chemical environment, species response, and community composition among different bodies of water. Physical and chemical factors other than sediment regulate the presence and distribution of aquatic organisms. Important factors are temperature, current velocity, substrate light, pH, dissolved oxygen, carbon dioxide, nutrients, metals, and pesticides. Many of these parameters are interrelated and may be confounded by sediment inputs. Light penetration and nutrient levels, for example, are strongly altered by sediment inputs, but nutrient levels are also a function of basin geometry and flushing rate (e.g., Tilzer et al. 1976).

Biological relationships, including competition and herbivory, are other factors which control the distribution and productivity of photosynthetic organisms. In higher organisms food requirements, species interactions, and biogeography also influence the occurrence of organisms. Thus, in evaluating the effect of sediment on aquatic biota, one must discriminate between effects due to sediment and those due to differences in the physical, chemical, and biological environment.

Water Velocity

One of the major difficulties in interpreting the impacts of sediment movement in streams is the intimate relationship between water velocity and sediment transport. Changes in water velocity alone are known to augment photosynthesis, supposedly by increasing the availability of nutrients and removing metabolic wastes (cf. Blum 1956; Whitford 1960; McIntire 1966a, 1966b, 1968; Hynes 1970a). Laboratory streams have been used to study the influence of a variety of factors on stream algae (McIntire et al. 1964; McIntire and Phinney 1965; McIntire 1966a, 1966b). The laboratory streams consisted of wooden troughs with bottom material from a nearby stream. Water was taken from a nearby stream and passed through the laboratory streams at a constant rate of flow. Light intensity, light-dark cycle, water depth, current velocity, flushing rate, and oxygen concentration could be regulated. This design provides an ideal situation for examining the effect of siltation under controlled conditions, as demonstrated by McIntire and Phinney (1965). They examined the effect of light intensity and carbon dioxide levels on periphyton production, respiration, and export. Extremely turbid conditions occurred in the laboratory streams with no change in water velocity during periods of high runoff in the stream used as a water source. Introduced silt apparently scoured the substrate, resulting in increased export of periphyton. The stream with higher light intensity (550 ft. candles) developed large growths of filamentous green algae (*Oedogonium* and *Ulothrix*) and showed the highest rate of export, 2.65 g/day, upon the first influx of silt. The stream receiving low light input, 225 ft. candles, developed a lower biomass of green algae and lost less material during the first silty period, 0.782 g/day. The ratio of production to respiration (P/R), which normally ranged between 1.3 and 2.5, dropped below one in both streams. This decrease in P/R ratio resulted from decreased rate of photosynthesis by the remaining algae and from greatly increased community respiration. Unfortunately, determinations of the amount of suspended material present were not made.

Flow Regime

Most rivers in the United States are regulated by impoundment and channelization. These changes alter the flow regime, sediment load, water temperature, oxygen content, and water chemistry, which often adds lentic plankton to downstream systems and alters the composition of aquatic biota in the impounded stretch. The results of impoundment often depend upon the mode of operation, particularly the flow pattern, depth from which water is released, and limnological conditions within the reservoir. Effects on downstream benthos have been reviewed recently by Ward (1967a). The diversity of benthos is invariably reduced below dams, and the composition often is altered greatly. Relatively constant seasonal flow patterns often result in increased benthic standing crops, while seasonal fluctuation in flows results in reduced benthic biomass. Daily fluctuations in flow seem to be less important than the seasonal regimes. Reduced benthic standing crops associated with variable flow may result from periodic exposure of the streambed or heavy silt deposition due to low flows or both.

Changes in the flow regime often result in changes in bottom fauna composition. Trotsky and Gregory (1974), for instance, found that changes in flow due to impoundment of the upper Kennebec River, Maine, modified the distribution of bottom fauna. Aquatic insects adapted for swift water were more abundant in the river above the reservoir than below it and were absent from those stations below the impoundment which had the lowest current velocity. Sampling stations above the impoundment averaged 19 genera of aquatic insects, while those below the dam averaged 11 genera.

The often noted increase in benthic standing crops below impoundments with seasonally constant flow may be related to greater food resources supplied by planktonic organism (Spence and Hynes 1971; Ward 1976a; Armitage 1978). Similar increases in standing crops, over the normal levels found in streams, are observed below outfalls from natural lakes (Hynes 1970b). A number of changes associated with impoundment and channelization of the Missouri River have been documented. Impoundment has increased the number of drifting crustaceans, with the invertebrate drift now composed of 50 to 80 percent *Leptodora kindta* (a limnetic cladoceran) by weight. Impounding also has reduced maximum flow and turbidity (from 4500 ppm to 50 - 70 ppm) and has resulted in higher dissolved oxygen concentrations. The increase in dissolved oxygen may be due to decreased organic loading because of the trapping of organic sediment in mainstream reservoirs and, hence, a lowered oxygen demand. Channelization, in conjunction with impoundment, has reduced both the size and variety of aquatic habitats by destroying key productive areas such as floodplain swamps, flood channels, and oxbows. The standing crop of benthos in channelized and unchannelized reaches is similar, but channelization has reduced the total benthic area by 67 percent. The construction of locks and dams and subsequent impoundment of the Arkansas River has increased the production and density of zooplankton (Short and Schmitz 1976). A decrease in zooplankton was noted downstream from impoundments as a result of the decrease in backwater areas and an increase in current velocity and silt load in the lower channelized reaches of the river.

Temperature

Impoundment alters the temperature regime of downstream areas as well. Storage reservoirs which release water from below the surface often result in lower summer temperatures, higher winter temperatures, more constant temperatures diurnally and seasonally, and delayed seasonal maximums downstream (Spence and Hynes 1971; Ward 1976a). Spence and Hynes report that impoundment of the Grand River (Shand Dam, Wellington County, Ontario) results in a four-week lag in summer rise in water temperature and a maximum temperature more than 6° C lower than upstream. Such temperature alterations may have important effects on stream biota. Hatching, growth, and emergence, for instance, depend on thermal cues. As a result, changes in thermal signals below impoundments may prevent or alter the completion of the life cycle (Hynes 1970b; Nebeher 1971; Lehmkuhl 1972; Ward 1976a, 1976b). Seasonal changes of as little as 2 to 3° C may effectively eliminate species by affecting body size and fecundity, and thus influence the geographic distribution of aquatic insects Sweeney and Vannote 1978).

Several other factors affect water temperature, hydrology, and sediment transport. Removal of riparian vegetation often increases temperatures and sediment loading. Mean monthly maximum temperatures increased up to 7° C following clear cutting in the forested coast range of Oregon (Brown and Krygier 1967). Similar results have been reported by Gray and Edington (1969) and Krygier et al. (1971). Leopold (1968) reported that streams on Long Island, most affected by man, exhibited temperatures 5° to 8° C above the control in the summer and 3° to 5° below in the winter. Land-use practices also control the amount of runoff and erosion. As a result, changes in fauna due to altered hydrologic and sediment regimes may be confounded by subtle changes in temperature.

9.1.4 Sampling Problems

The effect of sediment movement on macroinvertebrates, as with primary producers, is complicated by concurrent changes in many other environmental variables. Macroinvertebrates are mobile, resulting in difficulties in sampling and in interpreting changes in composition and standing crop. Explanations of variation in populations are further complicated by seasonal differences in reproduction, growth, and emergence (Hynes 1970b).

Quantitative estimation of standing crop is difficult, particularly since different sampling methods give different results (Gaufin et al. 1956; Cummins 1962; Hynes 1970a, 1970b; Chutter 1972; Dickson and Cairns 1972; Brinkhurst 1974; Hynes et al. 1974; Hughes 1975; Kinney et al. 1977). Macroinvertebrates have been found as deep as 54 cm below the surface in gravel beds (Coleman and Hynes 1970; Hynes 1974). Thus, conventional quantitative samples may underestimate standing stock and production, depending upon the type of substrate sampled. Furthermore, the number of samples required must be considered. For instance, it has been estimated that five surber samples, each one square foot, would give an estimate of the population of insects with a variability of ± 49 percent (Chutter 1972). Ten surber samples would reduce the variability of the sample mean to ± 27 percent for a confidence interval of 95 percent. The number of samples will, of course, vary with the distribution and abundance of the organisms sampled.

Other problems result from temporal and spatial changes in environmental conditions. Several authors point out that most available data are difficult to interpret because of arbitrarily fixed temporal and spatial sampling and a failure to account for temporal and spatial differences in hydrologic phenomena (Brinkhurst 1974; Livingston 1976, 1977; Hines et al. 1977). More detailed information regarding statistical methodology may be found in Edmondson and Winberg (1971) and in Elliott (1971).

9.2 INFLUENCE OF SEDIMENT ON AQUATIC PRIMARY PRODUCERS

Sediment may have the following effects on primary producers:

1. Reduces production by decreasing light penetration and by destroying photosynthetic organisms by abrasion, scour, and burial.

2. Changes species composition or relative abundances through changes in sediment type or composition.

Many of these conclusions are based upon field observations with their inherent difficulty in identifying causal relationships. As a result, qualitative statements regarding the effect of sediments on primary producers may be made, but quantitative predictions are difficult due to the complexity of aquatic systems.

9.2.1 Production

Light Penetration

It seems intuitive that increased turbidity from suspended sediments will decrease light penetration and result in lowered primary production. The reduction in light intensity by suspended solids results from scattering and absorption of light by the suspended particles. Several studies in the 1930s examined the effect of suspended solids on light penetration in streams and lakes.

Light penetration for over 700 stations in the Mississippi-Ohio-Missouri River drainages was reported in terms of the depth at which light would be reduced to one millionth of its surface intensity (millionth intensity depth or m.i.d.)(Ellis 1936). Measurements ranged from 84 mm for the Missouri River at Boonville, Missouri to 20,000 mm for the Tennessee River at Paducah, Kentucky. Lower measurements were related to an increased silt loading resulting from rainfall.

The theory of light scattering in natural bodies of water was described by Whitney (1938). Part of the light energy is absorbed by water, part is absorbed by suspended solids, and part is scattered. Whitney determined the total light extinction coefficient and the proportion of light scattered by solids in 15 Wisconsin lakes. The total extinction coefficient is composed of

$$Nt = N_w + N_{pc} + \frac{Ss}{2}$$

where N_w is the extinction coefficient of pure water, N_{pc} the coefficient for absorption by dissolved and particulate matter in the water, and Ss the coefficient for scattering. Since only half of the scattered light energy will be directed toward a light detector, Ss is divided by 2. Little correlation was found between the total extinction coefficient and the scattering coefficient since the scattering coefficient varies both with the concentration and type of particle. No studies were found relating concentrations and types of particles to scattering and extinction coefficients in freshwater systems, despite a theoretical basis for such measurements.

Variations in turbidity in western Lake Erie have been investigated, as they influence light penetration and the quantity of phytoplankton

(Chandler 1940, 1942a, 1942b, 1944; Chandler and Weeks 1945). In the spring, runoff from the western shore contributed large amounts of sediment from agricultural land. Comparison of weekly means for turbidity and discharge showed that increased river flow was accompanied by increased lake turbidities during the first six months of the year. During the remainder of the year, there were few periods of high discharge, but turbidities often increased due to high winds. Suspended inorganic material (clays, fine sand) varied from 1.0 to 28.5 mg per liter and composed from 50 to 95 percent of the total suspended matter. The inorganic portion was greatest during stormy periods when runoff, mixing, and turbidity were greatest; the organic portion was greatest during calm periods with little mixing, low runoff, low turbidity, and abundant plankton. Storms which mixed the water homogeneously to the bottom resulted in high turbidities (greater than 20 ppm in this case) and uniform light extinction with increasing depth. The suspended material settled during subsequent calm periods, resulting in variations in turbidity and light extinction with depth and time. Phytoplankton studies showed that plankton pulses occurred when turbidity was low; small populations existed when turbidity was high. Chandler suggested that variations in the composition, size, duration, and time occurrence of phytoplankton pulses may be partially accounted for by variation in turbidity. Verduin (1951, 1954) subsequently related turbidity, light penetration, nutrient levels, and phytoplankton standing crops to current patterns in western Lake Erie. Maps showing the horizontal distribution of light penetration were related to established current patterns. Most of the flow into Lake Erie (96 to 98 percent) is from the upper Great Lakes through the St. Clair-Detroit River (see Chandler 1944; Chandler and Weeks 1945). This water was low in suspended solids and nutrients. The balance was provided by rivers entering along the west and south shore. These rivers drain rich agricultural land and carry large loads of suspended sediment and nutrients. Verduin suggested that plankton in the clearer water to the northwest were limited by low nutrient levels. Maximal phytoplankton crops occurred when northeast winds mixed this clear water with the turbid, fertile water from the southwest, creating a water mass with increased fertility and intermediate turbidity.

Several other studies have attempted to relate phytoplankton standing crops to turbidity or light penetration. Conflicting results were reported in studies of Texas reservoirs by Harris and Silvey (1940). In two of the reservoirs studied, Worth and Bridgeport, maximum net plankton numbers occurred at low turbidities. Lake Dallas and Eagle Mountain Lake, on the other hand, had maximum net plankton numbers during high turbidities, but the quantity of organisms did not account for the opacity of the water. No one factor appeared to control the variability in plankton production, despite the large amounts of physical and chemical data gathered.

Claffey (1955) compared plankton standing crops in a series of farm ponds and reservoirs in Oklahoma. Twenty farm ponds were selected by matching a clear (turbidity < 25 JTU) and turbid (turbidity > 25 JTU) pond by similarity in surface area, watershed type, and locality. Twenty reservoirs, 10 clear and 10 turbid, also were examined. When the reservoirs and ponds were grouped according to their range in turbidities, the average number of plankters decreased with increasing turbidity. The range in plankton numbers shows little or no overlap among the turbidity categories. Similar results were reported by Buck (1956a, 1956b), with clear ponds (less than 25 ppm turbidity) producing eight times as much plankton as ponds of intermediate turbidity (25 - 100 ppm) and 12.8 times as much plankton as ponds with high turbidity (over 100 ppm).

It is commonly accepted that decreased light penetration due to increased levels of suspended solids will decrease primary production. This assumes that primary production is light-limited, but it may, in fact, be inhibited at high light intensities. Many algae have the ability to adapt to low light intensity or even require "shaded" conditions (McIntire and Phinney 1965; Tilzer et al. 1976). Furthermore, the effect of decreasing light intensities due to the presence of suspended solids may be modified by concomitant increases in nutrient levels (Verduin 1954; Sherk 1972; Tilzer et al. 1976).

The effect of sediment inflow on primary production has been examined in Lake Tahoe (Tilzer et al. 1976). Sediment inflow reduced underwater light intensities and increased nutrient concentrations simultaneously. Phytoplankton samples were incubated within and outside a sediment plume in order to compare photosynthetic rates under different light conditions. Surface samples incubated in clear water showed light inhibition throughout the day, but high subsurface light intensities resulted in increased photosynthetic rates with depth. Surface samples incubated within the plume exhibited light inhibition only around noon and decreasing photosynthetic rates with depth due to rapid light extinction. Integral photosynthesis was less within the sediment plume, despite reduced light inhibition at the surface, because of the decreasing photosynthetic rate with increasing depth. Bioassays also were conducted to compare photosynthetic rates under constant light conditions but with different nutrient levels resulting from sediment additions. These tests suggested that iron added by the sediment plume stimulated both photosynthetic activity and growth. The authors concluded that:

1. Increased turbidity alone reduces integral photosynthesis although this effect is diminished by less surface light inhibition.

2. Increased nutrient inputs alone lead to higher productivity.

3. The effect of combined sediment and nutrient inputs depends on the increase of biomass relative to the increase of non-living seston in influencing the portion of underwater light which is absorbed and utilized by the photosynthetic pigments of the algae.

A study of primary production in the Patuxent River Estuary illustrates the effect of gradients in nutrient availability, salinity, and light penetration in a flowing system (Stross and Stottlemyer 1965). Rates of primary production were measured along a 29 mile segment of the estuary and compared with light penetration, which increased downstream. The highest rate of carbon assimilation per unit volume occurred at the upstream end. The average rate of primary production from 14 sampling periods was 58.3 mg C/m^3/hr and ranged from 2.8 to 148.5 mg C/m^3/hr. The downstream, less turbid station was only one-third as productive on a unit volume basis, and also less variable. The average rate of primary production was 17.5 mg C/m^3/hr and ranged from 5.6 to 38.0 mg C/m^3/hr. The rapid quenching of light by suspended inorganics limited the depth of the eutrophic zone in the upstream reach so that it was least productive per unit area. At the extreme upstream station, one percent of the incident light reached one meter and the mean daily rate of primary production for the year was 1.2 g C/m^2. At the downstream station, one percent of the incident light penetrated five meters, and mean daily primary production was 1.8 g C/m^2.

The two previous studies address the interaction of nutrients and light intensity on rates of energy fixation by phytoplankton. Several other studies examine the effect of nutrients and suspended sediments on plankton composition.

Work on several reservoirs in northern Mississippi illustrates the complex changes in plankton composition due to changes in turbidity and nutrients (McGaha and Steen 1974; McGaha et al. 1976). Many plankton genera disappeared during periods of increased runoff and resulting higher turbidities. However, 7 of 27 phytoplankton genera studied responded positively to increasing turbidity, presumably due to some favorable change in nutrient or light levels. Drastic reduction in green and blue-green algal populations were commonly associated with high turbidity. As turbidity decreased, green and blue-green populations tended to increase and were correlated with orthophosphate concentrations. Diatoms, especially Melosira sp., increased during and after periods of high turbidity. Population increases by diatoms were correlated with silica levels which increased with the influx of siliceous material causing high turbidities. Some zooplankton, such as rotifers and microcrustaceans, also appeared to be positively correlated with increasing turbidity. McGaha and his co-workers concluded that no one factor was solely responsible for the observed fluctuations in plankton numbers.

A study of the phytoplankton of the Arkansas River yielded slightly different results, which may reflect differences between systems (McNutt and Meyer 1976). Decreased phytoplankton abundance was associated with high turbidities and attributed to decreased light penetration. Nutrients, grazing, and the influence of impoundments and tributaries also may have affected the phytoplankton assemblage. Contrary to the findings by McGaha and his co-workers, the green algae did not appear to be affected by turbidity, while several blue-greens and diatoms (including Melosira sp.) showed drastic reductions associated with high turbidities. Factors influencing the phytoplankton assemblage may vary from system to system; therefore, comparisons between systems must be made with caution (McNutt and Meyer 1976). Further interpretation of the study of McNutt and Meyer is hampered by the lack of nutrient data and information on the concentration, composition, and particle size distribution of suspended solids.

Few studies have examined the effect of reduced light intensities caused by suspended sediments on the photosynthetic rate of submersed macrophytes. Meyer and Heritage (1941) reported that the apparent rate of photosynthesis of Ceratophyllum demersum in western Lake Erie is reduced during periods of maximum turbidity, even at depths less than one mater. The compensation point was between eight and ten meters during a period of minimum turbidity and between one and two meters during a period of maximum turbidity. No inhibition of photosynthesis was noted at surface light intensities.

Several studies demonstrate a close correlation between the daily variation in light intensity and daily variations in photosynthesis by aquatic plants (Gessner 1938, 1955; Meyer 1939; Burr 1941; Verduin 1952; Westlake 1964, 1966a, 1966b). Many studies also relate the depth distribution of submerged macrophytes to limiting light intensities (Rickett 1921, 1924; Juday 1934; Wilson 1935). This suggests that photosynthesis by submerged aquatic macrophytes would be reduced by suspended sediment, but few data have been found regarding the importance of the effect.

From the preceding discussion, one may conclude that suspended solids have a great effect on primary production when they reduce light intensities. The overall result of sediment suspension will depend upon the degree to which light intensities are reduced and the length of time such conditions exist. Other factors may act synergistically or antagonistically with regard to reduced light levels. Under nutrient limited conditions, added nutrients may ameliorate the shading effect of suspended solids. Under enriched conditions, suspended soilds may influence nutrient availability and impose increased shading. The impacts of suspended solids are strongly dependent upon other factors, including temperature, current velocities and distribution, flow regimes, and taxon specific response by the biota.

Scour, Burial, and Abrasion

Erosion and deposition of sediment may damage algae and macrophytes. Erosion and deposition occur concurrently, so that separating their effects is difficult, if not arbitrary. During erosion, the substrate may be removed, carrying or detaching associated organisms. During deposition photosynthetic organisms may be buried by accumulating sediments. Abrasion, in the course of sediment movement also may be a significant cause of organism mortality.

Erosion of the substrate, or scour, often has a detrimental effect on benthic algae. Spring floods in areas producing large amounts of runoff may severely reduce algal populations and are probably a common annual pattern in areas with heavy snow accumulations (Hynes 1970b). Several studies indicate that the size of the bed material is extremely important in determining the extent of damage to benthic algae by high discharges. This is to be expected since bed load movement is partially a function of particle size, with smaller particles moving at lower water velocities than larger particles (Einstein 1964; Gregory and Walling 1973).

Douglas (1958) found that numbers of Achnanthes (a pennate diatom) were related to the stability of the substrate in Belle Grange Beck, England. Populations of 10^5 to 5×10^5 cells/cm^2 were quite common on permanent rock, and seldom fell below 5000 cells/cm^2 after high flows. Populations on stones occasionally reached 10^5 cells/cm^2, but were reduced to a few hundred cells/cm^2 after floods. High populations did build upon on the stones during periods of low flow. Similar results have been reported by Gumtow (1955) and Kobayasi (1961).

Tett et al. (1978) examined periphyton pigment densities in Meechums River, a low-alkaline, third order, piedmont stream in Virginia. Measurements of photosynthetic pigments (chlorophyll a and pheophytin a) were used to estimate the biomass of benthic algae on various substrates. The substrates included fine sand, silts, and clays, collectively referred to as mud (particle diameters less than 0.25 mm), sand (particle diameter of 0.25 mm to 4 mm), gravel (particle diameter of 2 mm to 75 mm), rock (from 4 cm upward), and muddy-sandy gravel, a heterogeneous mixture of mud and gravel. Pigment densities were related to substrate type and distribution, current velocity, and flow regime prior to sampling. Substrate type varied laterally and longitudinally due to differences in water velocity. Mean pigment densities and variability differed with substrate type. Chlorophyll a densities on mud, for example, appeared less susceptible to varying flow than those on sand. As a consequence, pigment densities on mud were less variable with time than pigment densities on sand. This was attributed to differences in the depositional environment, with mud being deposited along the edges of the channel in low velocity regions, and sand towards the center of the channel in high velocity regions. When discharge increased, chlorophyll a densities on sand often showed drastic decreases, while chlorophyll a densities on mud showed little change.

The authors made several important inferences based on the results of their study. First, it may not be useful to construct deterministic models to predict periphyton biomass in view of the stochastic fluctuation in biomass attributed to random changes in discharge and duration of low flows. Second, the response of periphyton biomass to changes in flow is a function of substrate type. It is not known whether periphyton on artificial substrates such as glass and plexiglass slides respond to flow, sedimentation, and bed load movement in the same way as do algae on natural substrates. Furthermore, the authors note that species composition and habit influence the relationship between flow, substrate, and chlorophyll a density. It also is evident that the effects of sediment movement are not readily separated from those due to changes in the flow regime.

Work by Tett and his co-workers adds to the understanding of the interaction of flow, substrate movement, and, indirectly, benthic algal biomass. The influence of these factors on rates of primary production by benthic algae is largely unknown. It has been suggested that scour reduces the epipelic community (organisms inhabiting the sediment surface) in Meechum's River (Virginia) and as a result decreases net community productivity (Kelly et al. 1974; Church, Kelly et al. 1978; Church, Shoop et al. 1978). As discharge and sediment movement decrease, the epipelic community becomes re-established, and net community productivity increases from day to day. No quantitative data has been published to date, however.

A study of the energetics of the Red Cedar River in Michigan indicated that autotrophic energy production and heterotrophic energy consumption decline significantly following high flows and siltation (King and Ball 1967). Energy budgets were constructed for five zones of the stream based on sampling during the summer of 1961. The fraction of allochthonous energy required by heterotrophic organisms varied from zero in the urban and reservoir zones to 91 percent in a reach below a sewage treatment plant. The amount of energy required by heterotrophs appeared to decline by 58 percent following high flows and heavy silt loads in September. Autotrophic aufwuchs production declined 68 percent during the same period. Macrophyte energy fixation, on the other hand, appeared unaffected. Turbidity reached 378 JTU during this period, compared to 20 to 30 JTU common for that time of year. The change in autotrophic production and heterotrophic consumption was attributed to siltation which might have resulted in reduced light penetration, scour, abrasion, and burial of organisms. These results must be interpreted with care because the Red Cedar River has been extensively modified by man and is influenced by effluents from metal processing and sewage treatment plants, runoff from agricultural and urban land, and an impoundment. Discharge also is quite variable, ranging from 3 to 6000 cfs within any year (Ball and Kevern 1973).

9.2.2 Species Composition and Abundance

The impact of sediment deposition on primary producers varies with the habitat requirements of the organisms, the type of material deposited, and the rate of sedimentation. These factors are not independent in that species requirements, sediment size and chemical composition, and rate of deposition are interrelated (Round 1964; Hutchinson 1975).

Attached algae and rooted macrophytes often develop best on specific substrates. Some require solid surfaces for attachment and may be affected adversely by the deposition of fine, shifting sediment. Others appear well suited for growth on beds of fine silt and clay. A third group, commonly growing on macroscopic plants are influenced by any changes in the condition of these plants (Blum 1956; Minckley 1963; Hynes 1970a; Nuttall and Bielby 1973). Changes in the proportion of various substrates will modify species composition, relative abundances, biomass, and productivity (Tett et al. 1978).

The response of primary producers to sediment type and changes in flow are species specific. Differences in algal species response to sediments and flow were reported in a study of Doe Run, Kentucky (Minckley 1963). Large mats of Vaucheria were common in softer substrates in areas protected from currents. They often were washed downstream during high flows and deposited on riparian objects. These emergent masses frequently remained alive and usually were able to fruit; fruiting did not occur in submerged mats. Dichostomosiphon tuberosus also was abundant and formed thick mats in silty areas. Dichostomosiphon was not affected as severely by floods as Vaucheria, presumably because of strong attachment to the bottom by densely interwoven rhizoids.

The distribution of primary producers was discussed in terms of the environmental gradient provided by Doe Run (Minckley 1963). Adjacent to the main spring, at the head of Doe Run, flow was swift and turbulent, with the moss, Fissidens jubianus dominating the rubble bottom. Next came an area with swift, almost laminar, flow and a bottom of sand and gravel. This area was dominated seasonally by Vaucheria, a rapidly growing alga which does not require a deep substrate for "rooting." This was followed by a transition area where deposition of larger sand and gravel size sediments occurred. This reach was occupied by Potamogeton foliosus, which anchors in coarse, unstable substrates by developing a substantial mass of subsurface rhizomes. A semi-lentic condition followed, where a milldam formed a pool on the stream. The substrate in this first pool graded from sand in the upper half to silt and muck near the dam and was colonized by Nitella flexilis.

Distribution and abundance of aquatic macrophytes in lakes is strongly influenced by physical and chemical characteristics of the substrate (Pearsall 1917, 1918, 1920, 1921; Misra 1938). The most abundant and varied communities occur on fine inorganic clays and silts and rich muds, especially in areas with low turbulence. The absence of turbulence may be due to water depth or dampening of water movement by the presence of macrophytes. In either case, resuspension of fine sediment, which may limit light penetration, is reduced.

Several studies demonstrate that the composition of the sediment is an important factor in the growth of macrophytes. Potamogeton perfoliatus and Elodea canadensis grew more rapidly in natural sediment than in sand (Pond 1907; Snell 1907). Similar results were reported by Mulligan and Baranowski (1969) for Myriophyllum exalbescens rooted in soil, as opposed to sand. Lobelia dortmanna grew only in sand with low amounts of organic matter in Big Lake, Minnesota (Moyle 1945). Organic sediment and sediment from alkaline, sulfate rich lakes inhibited growth; but water from these lakes did not hinder growth. Growth of Lemna, a free-floating, aquatic macrophyte, depended upon the amount of clay suspended in the culture and the type of soil from which it came (Healey and McColl 1974). Growth also was related to the amount of phosphorus added with the clay.

The effect of sediment deposition depends upon the rate of burial and the ability of the organisms to adjust to sedimentation. Pearsall's studies (1917, 1918) of English lakes indicate that some aquatic macrophytes do quite well in disturbed areas. Littorella, for instance, is a shallow water plant capable of colonizing wave-washed, sandy shores. Isoetes lacustris, on the other hand, was more common on stones covered by thin layers of silt, especially in areas with no erosion or deposition. Pearsall noted that Isoetes is readily smothered by sediment deposition since it apparently is unable to alter its root level. In cases where rapid silting was evident, Nitella and Juncus often occurred instead of Isoetes. In some instances Potamogeton perifoliatus replaced Isoetes in areas with increased silting. In those cases, the proportion of clay and concentration of potassium were greater in areas growing P. perfoliates than in those growing Juncus.

Many epipelic algae were well adapted for living on soft substrates. These include many diatoms, such as Nitzschia, Navicula, Caloneis, Gyrosigma, Surirella, Closterium, and Cymatopleura and motile canophytes such as Oscillatoria and Phormidium. These algae are capable of moving through sediment and often are found forming rich carpets on silt beds (Blum 1956; Hynes 1970a). Studies of tidal zone communities of pennate diatoms indicate that these algae move through sand at velocities ranging from 15 to 25 microns per second (Aleem 1950; Callome and Dekyser 1954; Wohlenberg 1954; Nultsch 1962). Motile unicellular algae may not be affected adversely when the overall rate of deposition is slower than their rate of migration. The energetic cost of movement, though, may reduce the potential for growth and reproduction.

Several sediment characteristics appear to regulate growth of aquatic macrophytes. These include: proportion of organic matter, silt, clay, and sand; pH; C:N ratio; exchangeable cations; redox potential; oxygen concentration; and nutrient availability (Misra 1938; Sculthorpe 1967; Hynes 1970a). These factors undoubtedly influence the type, amount, and productivity of algae, but no studies have examined these relationships (Hynes 1970a).

Sedimentation often results from lowered water velocities associated with plant structure. Large filamentous algae which grow attached to solid surfaces (Cladophora, Oedogonium, and Ulothrix) often accumulate silt as the water velocity is slowed within the thallus (Blum 1956; Minckley 1963). If enough silt accumulates, the lower portions of the organisms become shaded from light and subsequently may be killed or detached by the weight of the sediment. The remaining basal portion often initiates new growth under more favorable conditions.

The presence of macroscopic plants often causes local changes in water velocity. In rivers, growing shoots often cause reduced currents downstream, which lead to more deposition on the downstream side. The plant may continue to spread on the deposited material, protecting it from the direct force of the current and consolidating the material within a developing mass of roots or rhizoids. Eventually, the accumulating sediment and plant biomass increase turbulence and erosive force by diverting the flow around the growing bank (Minckley 1963; Hynes 1970a). The importance of this effect varies according to local conditions. In swift, deep rivers, plants will have little impact on the rate of sedimentation. In slow, shallow rivers, stands of plants may accelerate the building of silt beds, with silt-free channels forming between the accumulating mounds (Sculthorpe 1967). In lakes, the presence of aquatic macrophytes may reduce resuspension of bottom sediments by wave action (Jackson and Starrett 1959).

9.3 INFLUENCE OF SEDIMENT ON MACROINVERTEBRATES

There is a large body of literature treating the effects of sediment movement on macroinvertebrates. Aquatic insects receive the greatest attention, followed by crustaceans and molluscs. Other groups, including the Porifera, Coelenterata, Platyhelminthes, Annelida, and Bryoxoa have received less consideration. This may be due to difficulties in sampling and identification, restricted distributions, or to the relative insignificance attributed to some of these taxa.

Macroinvertebrates, particularly aquatic insects, have received much attention in terms of the biological effects of water pollution. They often are recommended as indicators of water quality (Hellawell 1972; Cairns and Dickson 1975) because a) keys are available for most groups, b) their relatively stationary habit allows spatial analysis of results, c) their relatively long life cycle makes temporal analyses possible, and d) their heterogeneous composition ensures that some groups will respond to a given environmental change. As a result, a large amount of information is available regarding the ecology of aquatic macroinvertebrates and their response to changes in water quality.

Variables controlling the distribution and abundance of macroinvertebrates have been reviewed in detail by Hynes (1970b), Brinkhurst (1974), and Wetzel (1975). However, interpreting changes in species composition, biomass, and number of macroinvertebrates does present certain difficulties despite the large amount of information available. Although aquatic macroinvertebrates are less mobile than fish, they may actively migrate from areas with adverse conditions. Invertebrates also have a variety of life cycles of varying durations, which must be accounted for in comparing changes in species composition, number of individuals, and biomass over time. The heterogeneous composition of macroinvertebrate communities may ensure that some change will be measured, but it may be difficult to ascertain the cause of a given response unless gross changes in their environment are evident.

Sediment movement is thought to influence macroinvertebrates by a) causing avoidance of adverse conditions by migration and drift; b) increasing mortality from sedimentation due to physiological effects, burial, and physical destruction; c) reducing rates of reproduction resulting from physiological effects, changes in suitable substrates, and loss of early life stages; and d) modifying rates of growth or production caused by habitat modification and changes in type and availability of food.

Few of these conclusions are based on controlled studies. As a result, changes often are documented without identifying the causative agents or without arriving at quantitative relationships between observed changes and hypothesized controlling factors. This does not negate the utility of the conclusions, but does point out a need for identifying the relative importance of the effects noted, an analysis of the multivariate nature of controlling factors, and, if possible, quantification of the observed relationships. Factors which affect the distribution and biomass of macroinvertebrates and which, consequently, may obscure the effects of sedimentation include: basin or channel geometry, water velocity, flow regime, temperature, pH, oxygen, carbon dioxide, salinity, interspecific competition, life history, predation, and accessibility of food. These variables must be kept in mind when examining the effects of sediments on macroinvertebrates.

9.3.1 Drift and Mortality

Numerous studies have shown that high rates of sedimentation often drastically reduce the numbers of benthic organisms, although it often is unclear whether the increased sedimentation increases mortality or increases drift of organisms from the affected area. Periods of maximum accumulation of sediment significantly reduced the standing crop of macroinvertebrates below the mouth of a logged watershed at Coweeta Hydrologic Laboratory (Tebo 1955). A flood occurring after the period of accumulation removed deposited sand and silt below the mouth of the logged watershed and reduced the density of bottom fauna to 7.3 organisms/ft^2, compared to 30.3 organisms/ft^2 at the upper stations not subject to siltation. Prior to flooding, samples below the logged waters had ranged from 22.8 to 27.3 organisms/ft^2. High flows from mid-February through May prevented reaccumulation of sand and silt at the lower station. During this period there was no significant difference in the bottom fauna of the upper and lower stations. Recolonization of the lower station was thought to have resulted from drifting insects.

A study by Gammon (1970) is particularly interesting since macroinvertebrate and fish populations were monitored over a four-year period, and the amount of sediment added to the stream was measured. Sediment was produced by the operation of a crushed limestone quarry and the amount added to Deer Creek (a small, low gradient stream in Putnam County, Indiana) was monitored using a 90° V-notched weir. No significant changes in chemical composition, oxygen content, or temperature of the creek water resulted from the introduction of sediment laden water. The sediment ranged from 5 to 125 microns in diameter and consisted of 90 percent calcium carbonate and 8 percent magnesium carbonate. Inputs which increased the suspended sediment concentrations less than 40 mg/liter caused a 25 percent reduction in macroinvertebrate densities in riffles below the quarry. Inputs that increased the concentrations to more than 120/mg/liter resulted in some deposition and caused a 60 percent decrease in macroinvertebrate densities. When sediment settled out in riffles, populations were reduced to 60 percent of normal levels regardless of the suspended solid concentration. The actual macroinvertebrate density ranged from 8 ind/ft^2 in riffles below the quarry to nearly 1000 ind/ft^2 in riffles above the quarry. When sediment inputs ceased, accumulated sediments were washed out by high discharge and macroinvertebrate populations increased to levels found in unaltered riffles within a few days. Experimental increases in suspended sediments increased the rate of invertebrate drift in direct proportion to the concentration added (up to 160 mg/liter). Drift appeared to be the primary cause of population decreases since no macroinvertebrate mortality was noted during the entire study. All species, including those preferring fine sediment, i.e., Chironomidae, Tricorythoides, decreased in numbers during sediment input. As a result, diversity, as measured by the index of Wihlm and Dorris (1968), remained fairly constant during changes in density.

Other studies show that macroinvertebrate populations and diversity are affected severely by sedimentation. Reed (1977) examined the response of macroinvertebrates and fish to siltation from highway construction in Virginia. Four streams were sampled upstream and downstream from construction sites. No other physical data were reported, but the streams appeared to be low gradient piedmont and coastal plain streams. The data indicated that siltation from highway construction decreased the number of species by 23 percent and the number of organisms by 40 percent. Single comparisons often showed significant differences in total numbers but not in diversity. Several observations were often necessary to detect significant differences in diversity. Although no quantitative measure of drift was made, the author suggested that drift is a major response of macroinvertebrates to increased siltation. Burial and subsequent mortality was not thought to be important. Recovery of macroinvertebrate communities was quite rapid and was attributed to the flushing action of high water and repopulation by drift.

Chisholm and Downs (1978) examined the effect of sediment movement on aquatic organisms in Turtle Creek, West Virginia. Turtle Creek is a high gradient stream in the southern Appalachians which was extensively altered by the construction of a divided four-lane highway. Sediment yield of Turtle Creek reached 34,000 T, or 1,400 T/mi^2 as a result of construction. Samples from Turtle Creek were compared with those collected on Lick Creek, an adjacent undisturbed stream. Changes in macroinvertebrates were evaluated in terms of diversity, total genera, and total organisms collected in a 45-minute period from three pools and three riffles at each site. Collections were made every four to five months at four sites. The greatest decrease in numbers and diversity was observed in the upper reaches of the stream where channel gradient was greatest and tributary inputs of organisms the least. This effect was attributed to high flow and erratic sediment movement. The number of organisms increased downstream and the range in diversity values decreased. The increase in macroinvertebrate numbers downstream appeared to be proportional to increasing drainage area, suggesting that drift from undamaged tributaries was important in repopulating damaged areas. A year after construction was completed, the number and diversity of macroinvertebrates in Turtle Creek were similar to those of Lick Creek.

Earlier studies have shown that increased sediment loading from mining and dredging operations is damaging to macroinvertebrate populations. Taft and Shapavalov (1935) found that macroinvertebrate populations were always lower in streams where mining occurred than in clear streams. Similar results were obtained by Sumner and Smith (1939) in their study of the effects of hydraulic mining in tributaries of the Yuba and American Rivers in California. Silted tributaries of the Yuba River had 63 percent of the standing crop found in clean tributaries. Silted tributaries of the American River supported only 41 percent of the numbers found in unsilted streams. Reaches of the Rivers Fall and Par (England) subject to heavy loads of china clay wastes supported 11 percent of the normal number of macroinvertebrates (Herbert et al. 1961). Unaffected reaches carried 60 mg/l of suspended solids, while polluted reaches had concentrations of suspended solids ranging from 1000 to 6000 mg/l. Solid wastes from a glass manufacturing plant on the Potomac River resulted in almost complete absence of organisms in areas with high rates of siltation (Bartsch 1959). Depression of benthic numbers was detectable as far as 13 miles downstream. Reduced numbers of macroinvertebrates also were found in downstream reaches of the Truckee River, California (Cordone and Pennoyer 1960). Silt from a gravel washing plant on a tributary caused a 95 percent reduction in benthic populations below the outfall. Populations were reduced to 25 percent of normal levels as far as 10 miles downstream. Numerous other references document decreases in macroinvertebrate numbers and biomass in streams with high rates of sedimentation [e.g., Cordone and Kelly 1961; European Inland Fisheries Advisory Commission (EIFAC) 1964; Gammon 1970].

The effect of sedimentation on benthos in lakes and reservoirs appears to be quite variable. High rates of deposition will occur where streams enter the basin and deposit their sediment load in the form of a delta. The greatest rate of sedimentation thus will be restricted to a few areas of inflow, and low rates of deposition will occur throughout the remainder of the basin. Complex spatial patterns often occur because of basin morphometry, currents, and wave action (Brinkhurst 1974). Effects of erosion and sedimentation on macrobenthos in northern Mississippi reservoirs were quite variable (Millican and McGaha 1969; McGaha and Steen 1974; McGaha et al. 1976). The mud-muck substrate produced by low levels of deposition on the profundal zone of the reservoirs provided the most suitable substrate for habitation by benthos. Deltas occurring where streams entered the reservoir were subject to increased deposition and erosion. These areas had fewer species and fewer numbers of organisms than the more stable profundal zone. Channelization of some streams resulted in extreme water level and water velocity fluctuations. Only shelled molluscs persisted in these areas.

Little evidence of actual sediment induced mortality exists. Many changes in macroinvertebrate communities have been attributed to mortality due to sedimentation, but without supporting evidence.

Sedimentation destroyed large portions of the mussel populations on the Mississippi, Tennessee, and Ohio Rivers (Ellis 1931). Populations were reduced where thick deposits of mud buried the adults or smothered the smaller mussels in areas where the adults could maintain themselves. Later work in experimental streams (Ellis 1936, 1937) showed that a variety of freshwater mussels could not tolerate the accumulation of one-quarter to one inch of silt on otherwise suitable substrates. Other individuals of the species thrived in the same water when they were suspended on lattice work a few inches or feet above the bottom. The high mortality was attributed to the accumulation of fine particles and not to low O_2, pH, CO_2, or other water conditions. Ellis noted that mussels in silty water remained closed 80 to 90 percent of the time and when opened produced excess mucus in order to remove silt which tended to settle in the mantle cavity. Individuals of the same species were closed only 50 to 60 percent of the time when in clear water. One would also expect changes in filtration rates of mussels exposed to suspended solids. This is supported by Stone and Palmer (1975), who found that the relative filtration rate of the bay scallop (Agropecten irradians) was related inversely to levels of clay minerals suspended in sea water. They also concluded that long-term exposure of bay scallops to sublethal levels of suspended solids may interfere with normal growth and development.

Mortality induced by suspended sediment may be related to the composition and size of the particles. Work reported by EIFAC (1964) showed that kaolinite and montmorillonite clays were harmful to Daphnia magna at levels of 82 and 102 mg/l, respectively. Charcoal was harmful at 82 mg/l, but pond sediment was not lethal up to concentrations of 1458 mg/l. The exact cause of mortality remains unknown, but Sabaneeff (1956) and EIFAC (1964) suggest that suspended solids may interfere with the feeding mechanisms of zooplankters. High suspended solid levels may result in silting out of zooplankton (Pennak 1946). This is supported by Hanks' (1976) finding that indiscriminant feeding on sediment particles by herbivorus zooplankton may increase organism density and result in loss by sinking.

Macroinvertebrate bioassays are often used to test for mortality caused by sediment. One must be careful to distinguish between chemical toxicity due to contaminants and mechanical injury due to solids in interpreting the results. Prater and Anderson (1977a, 1977b), for instance, exposed a number of organisms to sediment from Otter Creek, Ohio, and Duluth and Superior Harbor Basins, Minnesota, in a 96-hour bioassay. Test species included a burrowing mayfly (Hexagenia sp.), an isopod (Asellus communis), and a cladoceran (Daphnia magna). Sediment from several stations were found to be toxic, but the array of potentially toxic metals and pesticides present precluded determination of the cause of mortality. In several cases no mortality was noted, suggesting that chemical toxicity was more important than mechanical injury in bioassays with significant mortality. Oxberry et al. (1978) conducted long-term bioassays using taconite tailings from Silver Bay, Minnesota. Experiments with

Pontoporeia affinis, a benthic amphipod, and *Mysis relicta*, a freshwater opposum shrimp,showed no adverse effects. The authors concluded that no mechanical injury or chemical toxicity could be demonstrated for these inorganic sediments, but that high rates of deposition could be inimical to benthic populations near the waste outfall.

9.3.2 Reproduction

Few studies document the result of sedimentation on invertebrate reproduction. Various authors suggest that the loss of eggs and early instars results in significant changes in benthic macroinvertebrate communities, but it is difficult to collect, isolate, and identify eggs and early larval stages (Cummins 1962; Brusven and Prather 1974; Hart and Brusven 1976).

Experimental studies have shown that suspended solids have a variable influence on egg development in some invertebrates. Kaolin and illite suspensions have been found to reduce reproduction in planorbid snails (Harrison and Farina 1965). Of the three species used, *Biomphalaria pfeifferi* would not lay eggs in turbid water, *Bulinus globosus* layed eggs which aborted in turbid water but developed naturally in clear water, while reproduction by *Lymnaea natalensis* was unaffected by turbidity.

Aquatic insects may minimize loss of young due to high flows and sediment movement in two ways (Hynes 1970b). Eggs may be attached very securely to the substratum so that even if sediment movement occurs, some will survive. Many insect eggs also hatch over a long period of time, ensuring that short-term conditions which may decimate nymphs or larvae (e.g., floods) will not eliminate the species. Aquatic insects also lay eggs on or in emergent vegetation and in terrestrial habitats not subjected to extensive sediment movement or deposition (Merritt and Cummins 1978).

9.3.3 Habitat Modification

Sediment movement often modifies available macroinvertebrate habitats and alters the type, distribution, and availability of food. The preference of invertebrate fauna for certain substrates is an important aspect of faunal distribution and influences the impact of sediment movement on benthic communities. Interpreting the results of substrate changes is difficult due to problems in obtaining statistically accurate estimates of biomass and numbers, concomitant changes in numerous variables, differences inherent in substrate type, and the mosaic of substrate present (Hynes 1970a, 1970b; Harman 1972; Brinkhurst 1974; Hart and Brusven 1976; Minshall and Minshall 1977).

The type of substratum often controls the species composition, numbers, and weight of organisms present. Differences in number and species of invertebrates on different types of substrates have been demonstrated (Percival and Whitehead 1929). The largest number per unit area were found on thick moss; progressively fewer numbers were observed on *Potamogeton*, loose moss, *Cladophora* on stones, and on embedded and loose stones. Species composition also varied with the substrate. Similar results were obtained by Minckley (1963) in his study of Doe Run, Kentucky. In this case, number, biomass, and species composition were related to substrate. Changes in populations depended on the species as well as the substrate. High discharges, for instance, caused decreases in total number of organisms in beds of Fissidens, a moss, presumably due to wash-out of organisms and reduction in plant biomass. Amphipod populations, mostly Gammarus minus, often were constant, even after high discharge. Turbellaria, oligochaetes, and dipteran larvae increased in number in Fissidens beds during periods of above normal discharge. Minckley attributed this to movement of these organisms into the more stable habitat provided by the moss. Increases in oligochaetes and dipterans may have been related to increased deposition of sand and silt within Fissidens beds since ensuing low flows resulted in gradual decreases in silt and sand and reduction in oligochaete and dipteran numbers. Other substrates showed much greater fluctuations in total numbers, species composition, and specific populations. Shifting sand and marl riffles supported few organisms and were altered drastically by high flows and bed load movement. The close proximity of different substrates often influenced the distribution of organisms. The presence of isopods and amphipods on shifting sand, for instance, was attributed to dispersal from their optimal habitat, the Fissidens beds. In addition, some aquatic insects apparently change substrate preference as they mature. Minckley noted that early instars of Ephemerella and Baetis seemed to prefer the Fissidens, but then moved to open riffles as mature nymphs.

Substrate preference of macroinvertebrates is related to a variety of factors. The presence of vegetation often results in the greatest invertebrate biomass and may be related to increased surface area (Harrod 1964) or a sheltered habitat (Minckley 1963). The colonization of inorganic substrates may be a function of surface area (Sprules 1947; Barber and Kevern 1973), current velocity, particle size (Cummins and Lauff 1969; MacKay 1977; Minshall and Minshall 1977), degree of compaction (Hart and Brusven 1976), substrate stability (Percival and Whitehead 1929; Chutter 1969), amount and type of detritus, (Egglishaw 1964; Woodall and Wallace 1972; Minshall and Minshall 1977; Rabeni and Minshall 1977), and the amount of periphyton (Minshall and Minshall 1977). In addition, organism preferences may change with different stages in the life history (Minckley 1963; Harmon 1972; MacKay 1977). Unfortunately, the factors listed are not independent, resulting in difficulty in experimental design and interpretation.

For example, benthic insect communities in six first- and one second-order streams in the easily eroded Idaho batholith were compared to determine the degree of natural variation within and between streams and seasons (Hart and Brusven 1976). Higher flows during spring runoff of the second year of the study decreased the standing crop, species diversity, and total numbers of species present in all streams. High runoff resulted in larger surface substrate particle size, greater cobble exposure, lower amounts of detritus, and lower insect populations than found after the low spring runoff of the previous year. Mayflies (Ephemeroptera) were the most adversely affected group and stoneflies (Plecoptera) the least. Ordinal dominance of insects changed to a great degree in some streams but little in others over the summer; communities did not change in the same way in each stream. The authors attributed these changes to differences in location, microhabitat, flow, substrate, channel configuration, intra- and inter-specific competition, food type and availability, and dissolved substances. This study illustrates the variability in community responses found and the complex set of interactions which may cause these changes.

Several studies document changes in macroinvertebrate communities due to substrate alteration by siltation. The elimination of aquatic plants by turbidity may be the primary effect of sediment loading and the elimination of insects only a secondary effect (Surber 1953). This is supported by Hamilton (1961), who suggested that high turbidity produced by suspended inorganic sediment may not, by itself, harm the bottom fauna in shallow lotic environments unless the bottom becomes covered with a thick layer of such material. Settling out of suspended solids may alter or destroy the vegetation and result in a change in the associated fauna before smothering of the "normal" substrate can occur. Other studies, however, suggest that changes in the bottom faunal community are quite evident at low levels of sediment input and that drastic changes occur before smothering of the normal substrate (Chutter 1969; Gammon 1970).

Few studies have been detailed enough to show whether particular groups of invertebrates were affected more by siltation than others (Chutter 1969). Many studies have shown that faunal density may decrease considerably, but few revealed whether fauna associated with fine sediment (e.g., Tubificidae and Chironomidae) appeared. Chutter's work on a South African river demonstrated that the invertebrate fauna of sediment and cobble substrates changed with the amount of silt and sand in the water course. In reaches with large amounts of silt and sand, the variety of animals found in cobble substrates decreased, but the total faunal density did not change. Some of the organisms which were affected adversely by sedimentation appeared in large numbers below impoundments which trapped silt and sand. Seasonal changes in flow also were important, with higher flows and large amounts of silt and sand causing summer declines in surface dwelling organisms as a proportion of the entire sediment fauna. Chutter concluded that there may be a considerable change in the composition of cobble fauna due to silt and sand inputs without the substrate being smothered. This increase in the amount of silt and sand results in increased instability of the substrate and sealing of interstitial spaces.

9.3.4 Avoidance and Refugia

Macroinvertebrate responses to sediment loading must take into account avoidance of adverse conditions and later recolonization from refugia. Changes in faunal numbers and composition may result from migration to more protected habitats or drift from the affected area during adverse conditions. Following the resumption of "normal" conditions, altered areas may be recolonized by drift from unaffected upstream areas and active migration from refugia.

The importance of drift often is emphasized in studies of sedimentation in streams. A number of studies suggest that the observed decline in numbers of invertebrates in response to suspended solids results from drift out of affected areas (Gammon 1970; Rosenberg and Wiens 1975; Chisholm and Downs 1978).

Drift is increased during periods of increased flow. Anderson and Lehmkuhl (1968) found a fourfold increase in numbers and five to eightfold increase in biomass of drifting organisms with rainfalls of less than one inch. The number of insects drifting per unit volume was thought to be similar before and during freshets, hence the observed increase may be attributed to increased volume of flow (Elliott 1967). The authors suggested that drift may be beneficial in dispersing aggregates of young larvae, but that the removal of leafpacks and detritus could be detrimental for the benthos. In addition, macroinvertebrates may migrate to protected habitats during adverse conditions (Minckley 1963).

The hyporheal habitat (below the sediment surface) may provide another refugium from extreme conditions. Extremely high discharges in a Welch mountain stream severely depleted the insect fauna (Hynes 1968). Following resumption of normal flow, the fauna steadily increased with the same size distribution as before the high flow. This suggests that recolonization occurred by migration from within the gravel bed and not from reproduction. Subsequent work (Coleman and Hynes 1970; Hynes 1974) confirms that invertebrates may occur down to at least 50 cm in gravel beds. In addition, Coleman and Hynes (1970) found that only 20 percent of the total number of organisms sampled occurred in the first 7.6 cm. Conventional samples, e.g., surber sampler and standardized netting,may seriously underestimate standing crops of macroinvertebrates in gravel substrates since only the upper few centimeters are sampled. The importance of the hyporheal zone as a refugium is unknown, as is the result of surface sealing by the fine sediments (Chutter 1972; Hart and Brusven 1976).

Drift from unimpacted upstream areas is thought to be a major source for recolonization by invertebrates. Downstream drift of Baetis (a mayfly) and Gammarus (an amphipod) was sufficient to replenish reduced populations to normal conditions within one or two days when drift rates were high (Waters 1964). Many studies suggest that recolonization by drift is quite rapid following resumption of normal conditions (Gammon 1970; Reed 1977; Chisholm and Downs 1978).

Upstream movement by invertebrates also has been noted. Upstream movement of benthos in the Speed River, Ontario, was 6.5 percent of downstream drift by numbers and 4 percent by weight (Bishop and Hynes 1969). Upstream movement may account for recolonizatin of denuded areas but is not of the same magnitude as downstream drift. The ability of invertebrates to move upstream is related to the substrate type. Heavy sand accumulations impede upstream movement of many common riffle insects, even at water velocities as low as 12 cm/sec (Luedtke and Brusven 1976). As a result, sand deposition in gravel and cobble beds may block this upstream movement by invertebrates. Williams and Hynes (1976) and Williams (1977) evaluated the relative importance of four means of recolonization in permanent and temporary streams: downstream drift, upstream migration, vertical migration from within the substrate, and aerial sources, e.g., oviposition. In the permanent streams, all four sources contributed substantially, with drift being the most important. In temporary streams, vertical migration was most important, accounting for as much as 95 percent of the increase in numbers. The relatively low importance of oviposition by adults was related to seasonal aspects of reproduction. The authors noted that it is difficult to separate the effect of vertical migration from subsequent upstream migration and downstream drift.

Colonization of disturbed areas in lakes also appears to be quite rapid

Clean substrates placed in Lake Windermere were colonized by several species in as little as six hours (Moon 1940). As the time allowed for colonization increased, the number of species and number of individuals also increased.

9.4 INFLUENCE OF SEDIMENT ON FISH

Studies of the effect of sediment movement on aquatic biota often are initiated because of concern for fisheries resources. Much of the work in this area deals with salmonid fisheries, hence conclusions regarding the effect of sedimentation on fish are largely oriented toward cold water fisheries (cf. Cordone and Kelly 1961; EIFAC 1964). Recent work documents changes in warmwater species, but less information is available for these organisms than for salmonids. The general conclusion is that sediment loading may increase adult mortality, decrease rates of reproduction, and modify growth rates of fish.

9.4.1 Mortality

Increased mortality of adult fish may result from abrasion and smothering of gill tissue by fine sediment. This conclusion is based on two lines of evidence 1) exposure of fish to suspended sediment under laboratory conditions and 2) examination of fish collected in field surveys. The most widely-cited laboratory study is Wallen's (1951) investigation of the direct effect of suspended soil on warmwater fishes. Wallen exposed 380 individuals of 14 genera and 16 species to varying concentrations of soil in aquaria. No estimates of suspended sediment concentrations were made. The author found that 1) noticeable behavioral reactions did not begin until turbidities reached 20,000 JTU; 2) most of the experimental fish endured more than 100,000 JTU for a week or longer, and 3) fish died at concentrations producing 175,000 - 225,000 JTU due to clogging of the opercular cavity and gill filaments with sediment. No evidence of gill injury or unusual amounts of mucus was found in the dead individuals. The tolerance of the fish to high levels of suspended sediment in aquaria led Wallen to conclude that natural clay concentrations were not likely to be lethal for juvenile and adult fishes. Wallen recognized that turbidity is an optical property, and, hence, the actual concentrations in the aquaria remain unknown. The concentrations and particle sizes (24 - 62 μ) also varied with time because of the periodic stirring and subsequent decrease in concentration and particle size as the solids settled. In addition, no food was added during the experiments because such additions decreased both the turbidity and oxygen concentration. Thus, mortality may have been induced by the poor condition of the fish after extended starvation.

Several researchers suggest that suspended soils adversely affect the gills of adult fish. The effect depends upon the type of particle, its size, shape, hardness (Ellis 1944), and the length of exposure (Herbert et al. 1961; Herbert and Merkens 1961; Herbert and Richards 1963). Exposure to solids such as rock powders, cinder particles, kaolin, diatomaceous earth, and coal washings may abraid gills, induce mucus secretion, cause thickening of the epithelial cells, and reduce resistance to disease (Herbert et al. 1961). Herbert and Merkens (1961) studied the impact of kaolin and diatomaceous earth on rainbow trout survival in aquaria. No difference in effect was found between kaolin and diatomaceous earth. Mortality was extremely variable; exposure to low concentrations had some adverse affect, but not nearly as great a mortality as at higher concentrations. No significant difference was found between either the weights or the lengths of the fish exposed to different concentrations. Examination of gill tissue showed that some individuals exposed to higher concentrations developed thickened epithelial cells; others exposed to these suspensions for three to six months showed no thickening of epithelial cells or other obvious changes in gill structure. The authors noted that rainbow trout had increased incidences of fin rot when exposed to suspended solids. They concluded that inert suspended solids may reduce survival in rainbow trout by potentiating other stresses such as disease or changes in gill structure, which otherwise would have negligible effects on the fish. This is supported by histological studies which demonstrate changes in gill structure in other fish species affected by fine suspended soils (brown trout, Herbert et al. 1961; white perch, O'Conner and Sherk 1975). Thus, there is some evidence that suspended solids may have sublethal effects on adult fish. Evidence for directly induced mortality is based on fish exposed to extreme concentrations, where avoidance of adverse conditions is impossible (e.g., aquaria). Documentation of sediment-caused mortality under natural conditions is complicated by the avoidance of turbid conditions by many fish (Gammon 1970), the possible presence of contaminants (Cordone and Kelly 1961; Legore and Desvoigne 1973), and the ability of healthy, uninjured fish to wash away sediment particles through the continuous secretion of mucus (Ellis 1937). Several studies have found that salmon will migrate through silty water from glacial streams (Smith 1939; Foskett 1958; Cooper 1965) and mining activities (Ward 1938a, 1938b) to spawn in clear tributary streams. It is more likely that fish populations will be reduced by destruction of their food supply, alteration of their habitat, or reduction in reproductive success before direct effects of suspended sediment will be detected.

9.4.2 Reproduction

One of the major impacts of sedimentation on fish populations appears to be disruption of normal reproduction (Cordone and Kelly 1961). Sedimentation may impair reproduction directly by increasing the mortality of eggs and fry or indirectly by altering habitats so that reproductive behavior, such as nest building, does not occur.

Early studies of the effect of sedimentation on fish reproduction were concerned with the hatching of salmonid eggs in gravel. One of the earliest experiments documenting the influence of sedimentation on fish egg survival was by Harrison (1923). He found that the survival rate of salmon and trout eggs placed in man-made redds (nests) declined as the particle size of the substrate decreased. Later studies considered conditions necessary for natural propagation of salmonids in gravel beds. These studies involved comparing the survival of eggs incubated in gravel in a hatchery trough with those incubated in a hatching basket. Experiments with steelhead trout, Salmo gairdnerri (Shapavalov 1937), and coho salmon, Oncorhynchus kisutch (Shapavalov and Berrin 1940), showed that silt produced by high flows was deposited in the gravel, smothering the eggs and preventing the fry from emerging.

A subsequent study of Shaw and Maga (1943) demonstrated that the timing of silt addition is critical in terms of reproductive success. Coho salmon eggs (O. kisutch) were placed in gravel nests in three standard hatchery troughs. The control trough received only normal hatchery water during the experiment. The experimental nests received mining silt for varying periods and at different times during development. At the end of the experiment, the controls yielded an average of 16.2 percent fry (total number of fry emerging from each nest divided by the number of eggs introduced); the nests receiving silt from the beginning of incubation averaged 1.16 percent emergence; and the nests receiving silt after the incubation period yielded 13.4 percent fry with yields declining with earlier initial dates of silt addition. Thus, silt addition during incubation drastically reduces survival. Additions after hatching may reduce emergence, but do not have as severe an effect on the yield of fry. The authors also pointed out that flow conditions are important. During periods of high flows, most clay and silt size particles will be in suspension. As a result, little deposition will occur and minimal damage to eggs in the gravel would be expected. During periods of low flow, added sediment would be deposited in gravel beds and the survival of eggs and emergence of fry would be reduced.

A number of factors influence the survival of salmon eggs and fry in gravel. The uniformity of particle sizes and proportion of fine particles (less than 300 µ) affects the apparent rate of flow through the bed (Cooper 1965). The rate of flow through the gravel bed affects oxygen concentrations, the level of metabolic wastes, and, as a result, the survival of eggs and fry (Alderdice and Wickett 1958; Peters 1962, 1967; Cooper 1965). The occurrence of high flows may result in scouring of the bottom, destroying eggs and young fish (Allen 1951; Wickett 1958; Onodera and Ueno 1961; Elwood and Waters 1969; Hoopes 1975). Low flows may prevent access to spawning areas, prevent flushing of accumulated silt, and result in superimposition of redds (Wickett 1958). Turbid conditions, resulting from mining or dredging, also may cause salmon to crowd into clear areas to such an extent that spawning individuals destroy previously constructed nests (Smith 1939; Cooper 1965).

Very little information has been found regarding the effects of sedimentation on reproduction by warm water fishes. Several researchers have noted that small headwater streams, which are the most susceptible to alteration and sedimentation, are very important in maintaining fishable populations in larger streams, rivers, and lakes. Headwater streams serve as important breeding grounds and also provide habitat for growth and reproduction of smaller fish and invertebrates used for food by game species (Hall 1972; Smith 1972; Karr and Gorman 1975). Gammon (1970) found that longear sunfish (Lepomis megalotis) spawned in clear water with a clean gravel substrate, but avoided areas with deposits of a thin white layer of sediment from a limestone quarry. There was no indication that spawning of other species, such as suckers, was inhibited by introduced sediment.

Environmental factors regulating northern pike (Esox lucius) reproduction were studied in two main-stem impoundments on the Missouri River (Hassler 1970). Silt deposition of 1 mm/day due to bank slumping and wave action resulted in egg mortalities in excess of 97 percent. Once hatching occurred, siltation had less of an effect. Suitable spawning substrate also was necessary, with large year classes occurring when abundant flooded vegetation was available for egg deposition. Small numbers in a given year class occurred when the only available substrate was mud or rubble.

Much less research appears to have been done on the influence of siltation on reproduction in groups other than the salmonids. Life history and ecological requirements are known for most fish; thus, one may suggest that reproduction in certain groups will be impaired by siltation. This is true especially for those groups requiring vegetation (e.g., Esocidae) or clean gravel or rock substrates for reproduction. Others are tolerant of silt turbidity and may replace clear water species (Ritchie 1972).

9.4.3 Fish Production

Sediment loading may regulate fish populations indirectly by modifying available habitats and thus altering rates of fish production. This may result from loss of habitat, decreases in the availability of prey, or from behavioral changes in the fish. Several researchers suggest that fish populations often are limited by the amount of production within a system, as opposed to limitation of predator species by physical parameters (Herbert et al. 1961; Lotrich 1973). Good evidence exists, on the other hand, that reproduction is affected by physical conditions, and that physical factors control the distribution of fish in many cases (McCrimmon 1954). One must conclude that fish production is controlled by a myriad of factors, with the most important factors depending upon the site and species studied, as well as the time of study.

Siltation of riffles appears to be a critical factor in the survival of some juvenile fish. A detailed study by McCrimmon (1954) considers several factors affecting the survival of Atlantic salmon fry (Salmo salar). Fry were planted in Duffin Creek, a stream flowing into Lake Ontario, and their survival and distribution monitored over a five-year period. Factors affecting survival included temperature, turbidity, predation, shelter, flood, sedimentation, and food. Observation of the fish from the time of planting until their descent from the stream showed that the population of salmon supported in a section of the stream was dependent on the type of habitat, and that the required habitat changed as the fish grew. Freshly planted fry had the greatest survival in shallow gravel riffles, where shelter was available in spaces among gravel and stones. Those fry planted in pools, or moving to pools from unsuitable riffles, were subject to intensive predation by brook trout (Salvelinus fontinalis), creek chub (Semotilus atromaculatus), and common shiner (Notropis cornutus). As the salmon increased in size, their habitat requirements changed from shallow riffles to deeper pools with shelter offered by undercut banks, logs, rubble, and vegetation. Some yearling salmon were forced to move out of the tributary streams into the main stream, where more suitable habitats existed. The amount of sedimentation in the riffles also influenced salmon survival. Three types of bottom were considered: totally sedimented, with the original gravel or rubble covered with sediment; heavily sedimented, with the spaces around the gravel and rubble filled in with sediment; and unsedimented, with the spaces around the gravel or rubble not filled in with sediment. As the amount of sedimentation increased in the riffle areas, the protective cover for the fry decreased and salmon survival showed a corresponding decline. The inability of some sections to support yearling fish also was attributed to sedimentation and resulting loss of cover in pools. Similar findings have been reported for juvenile steelhead trout (*Salmo gairdnerri*) and chinook salmon (*Oncorhynchus tshawytscha*)(Stuehrenberg 1975), but neither McCrimmon nor Stuehrenberg suggested that reductions in prey species were important.

Lotrich (1973), on the other hand, found that reduction in prey species may be important. Lotrich studied the factors affecting the fish community in first-, second-, and third-order reaches of Buckhorn Creek, in eastern Kentucky. The species composition increased longitudinally with increasing stream order. Species in the first-order stream fed primarily on terrestrial invertebrates falling into the streams. Aquatic primary producers and aquatic invertebrates became important energy sources in second-order streams. Fish, salamanders, and invertebrate detritivores were utilized in the third-order stream. During the study, silt from a strip mine entered the third-order stream and had an adverse effect on the fish community. The number of fish declined by 50 percent and biomass by 10 percent. This reduction appeared to be due to siltation, as no changes in pH were found. The reduction in numbers occurred primarily in those species utilizing aquatic invertebrates and in age group I of all species. Age groups II and III of the larger species were not affected as severely, but production in those groups was expected to decline as there would be fewer age group II individuals from those few surviving in age group I. No change occurred in the number of fish in the unaffected second-order segment immediately above the polluted third-order reach. The reduced numbers may be attributed to three factors: a reduction in available food for species using aquatic invertebrates, avoidance of turbid conditions, and loss of refugia necessary for the survival of smaller individuals.

Several studies suggest that floods may reduce the numbers of juvenile fish (age class 0 +), but that reduced invertebrate fauna exert a longer lasting limit on fish production (Allen 1951). A more recent study by Elwood and Waters (1969) demonstrated that reduced invertebrate populations, due to severe flooding, caused an apparent decrease in growth rate for a population of brook trout (*Salvelinus fontinalis*) in a Minnesota stream.

Fish respond to increased sediment inputs in several ways. Response appears to be species specific and may include reduced feeding, increased ventilation rates, and avoidance of adverse conditions.

Suspensions of iron hydroxide reduced the growth rate of juvenile brook trout (*Salvelinus fontinalis*), presumably as a result of impaired visibility which prevented the fish from feeding (Sykora et al. 1972). O'Brien (1977) measured the reactive distance of bluegills (*Lepomis macrochirus*) to various sizes of *Daphnia pulex* under different light intensities and turbidities. The reactive distance, the greatest distance at which a predator can locate its prey, was greatly reduced by both reduced illuminance and increased turbidity for all prey sizes. This factor may be very important since a 50 percent reduction in reactive distance may reduce the actual volume searched by a factor of 8 if the fish searches a hemisphere (O'Brien et al. 1976).

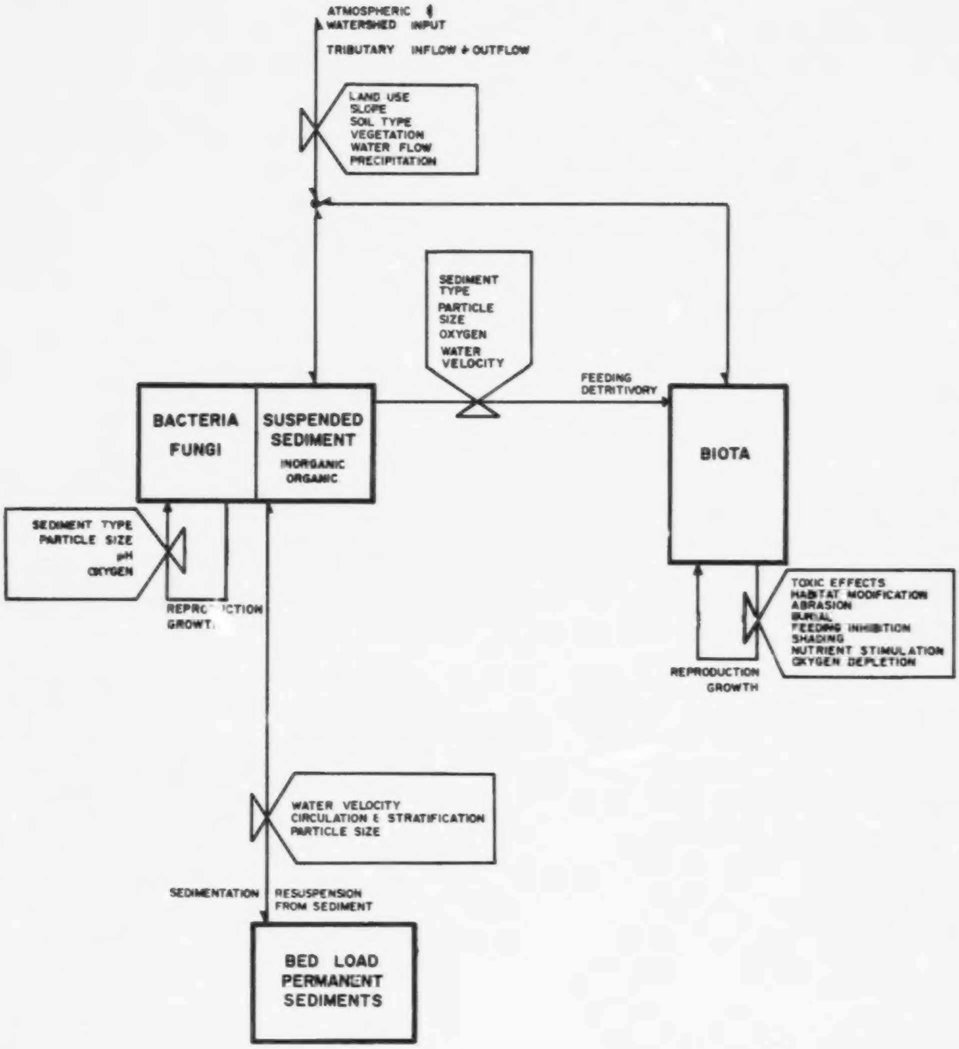
Increased turbidity results in other behavioral changes as well. General movement by largemouth bass (*Micropterus salmoides*) and green sunfish (*Lepomis cyanellus*) was reduced when turbidity was elevated for 30 days in aquaria (Hemistra et al. 1969). The normal social hierarchy of the green sunfish was disturbed during periods of elevated turbidity. There were no significant differences in the number of attacks or amount of food eaten by either species. The absence of a change in feeding behavior may be due to the light intensity used, which was not reported (Vinyard and O'Brien 1976). A field experiment by Bachman (1958) demonstrated that cutthroat trout (Salmo clarki) ceased feeding and moved to cover when turbidity was increased to 33 ppm. Horkel and Pearson (1976) found that green sunfish (Lepomis cyanellus) responded to clay suspensions by increasing their ventilation rates. The fish were examined at four temperatures (5, 15, 25, and 35° C) and six bentonite clay concentrations (0, 3.3, 6.7, 13.3, 17.8, and 26.7 g/l). At 15 and 25° C, ventilation rates increased 50 to 70 percent for the three highest concentrations. Rates of oxygen consumption were not affected by turbid suspensions at any of the four temperatures. The authors suggest that increased ventilation rates are a means of compensating for reduced respiratory efficiency under turbid conditions and also may prevent clogging of the gills with clay. A decline in activity also was noted following the introduction of the clay suspensions.

Several authors have noted that fish exposed to turbid suspensions often show reduced activity (Bachman 1958; Heimstra et al. 1969; Horkel and Pearson 1976). This reaction has been noted only under controlled conditions. Salmonids, for instance, often migrate through stretches of turbid water (Cooper 1965). Other work suggests that fish actively avoid turbid conditions, a response that is probably species specific (Gammon 1970). Juvenile Atlantic salmon often seek out turbid water produced by disturbing the bottom (McCrimmon 1954). McCrimmon suggested that poor visibility may protect the juveniles from predation and noted that the smolts descend streams during periods of high water and low visibility.

The distribution of fish has been related to sediment produced turbidity. Young largemouth bass (Micropterus salmoides) were not found in waters with turbidity greater than 84 ppm; redear sunfish (Lepomis macrolupus) were absent where turbidity exceeded 174 ppm; and bluegill (Lepomis macrochirus) were not found in water with more than 184 ppm turbidity (Buck 1956a, 1956b). Fish yield also was correlated with turbidity. Clear farm ponds produced 1.7 to 5.5 times the total weight of fish obtained from more turbid ponds. This may be due to lower primary production in turbid ponds since clear ponds had plankton standing crops 8 to 13 times greater than more turbid ponds. In addition, a number of monographs document the preference of fish for clear over turbid waters (Trautman 1957; Pflieger 1971; Buchanan 1976).

9.5 SUMMARY

Considerable effort has been directed toward determining the effect of sediment inputs on aquatic biota. While a number of general conclusions can be drawn from the literature, the number of interacting variables often precludes quantification of causal relationships. Figure 9.1 summarizes the major interactions between biota and sediments. However, interpreting the response of aquatic biota to sediment inputs is difficult since different bodies of water vary in their physical, chemical, and biological characteristics. These physical, chemical, and biological factors may act synergistically or antagonistically with sediment in regulating the presence and abundance of



ATMOSPHERIC &
WATERSHED INPUT
TRIBUTARY INFLOW & OUTFLOW
LAND USE
SLOPE
SOIL TYPE
VEGETATION
WATER FLOW
PRECIPITATION
SEDIMENT TYPE
PARTICLE SIZE
OXYGEN
WATER VELOCITY
FEEDING
DETRITIVORY
BACTERIA
FUNGI
SUSPENDED SEDIMENT
INORGANIC
ORGANIC
BIOTA
SEDIMENT TYPE
PARTICLE SIZE
pH
OXYGEN
REPRODUCTION
GROWTH
TOXIC EFFECTS
HABITAT MODIFICATION
ABRASION
BURIAL
FEEDING INHIBITION
SHADING
NUTRIENT STIMULATION
OXYGEN DEPLETION
REPRODUCTION
GROWTH
WATER VELOCITY
CIRCULATION & STRATIFICATION
PARTICLE SIZE
SEDIMENTATION
RESUSPENSION
FROM SEDIMENT
BED LOAD
PERMANENT
SEDIMENTS

Fig. 9.1. Sediment exchanges and interactions in aquatic systems. Major biotic and sediment pools are shown in compartments. Lines indicate material flows, with the controls on these flows also indicated. Single-headed arrows are used when the opposite directions of flow are labelled.

organisms. Therefore, grouping of waters by generally similar physical, chemical, and biological properties, as may be accomplished by a regionalization scheme, may be useful for predicting impacts by sediments at the various hierarchical levels.

9.5.1 Sediment Impact on Trophic Levels

Primary Producers

Sediment influences primary producers by altering light intensities, nutrient levels, substrate types, and species composition. The response of primary producers is often stochastic, depending upon random changes in flow and, hence, sediment movement. Overall, increased levels of suspended sediment reduce light intensity and limit photosynthesis; however, the presence of associated nutrients may ameliorate this effect to some extent. Species composition of primary producers also is influenced by suspended and deposited sediment. Changes in species and biomass are related to changes in suspended solid concentrations, rates of deposition, bed load movement, and substrate type. Predictive information relating the response of primary producers to sediment characteristics is lacking. Research using controlled experiments, such as laboratory streams, appears promising. The development of better techniques for estimating primary production in field situations and analyzing the response of primary producers to the hydrologic regime is necessary.

Macroinvertebrates

Sediment influences macroinvertebrates by modifying habitats and inducing movement out of areas with high rates of deposition. High rates of deposition often drastically reduce the number of benthic organisms by burial of sessile organisms and alteration of the substrate. Increased suspended sediment levels often result in increased insect drift in running water. Filter-feeding invertebrates, especially certain molluscs and crustaceans, are adversely affected by high levels of suspended solids for extended periods. There is little evidence for sediment-induced mortality for groups other than the molluscs. Recovery by mobile invertebrates is rapid,following the resumption of normal conditions. Recovery depends upon how the habitat was modified, the substrate preference and life history of the organism, the types of refugia available, and the mode of migration. Recolonization may involve downstream drift, upstream migration, vertical migration from within the substrate, and reproduction. Little is known of the importance of the hyporheal habitat, the result of surface sealing, and the effect of sediment loading on reproductive success.

Fish

Sediment affects fish by indirectly, increasing mortality, altering rates of reproduction, and modifying growth rates. Suspended sediment does not appear to be lethal for juvenile and adult fish, but may reduce their resistance to disease and damage gill tissue. Fish may avoid localized areas of increased sediment concentrations. The deposition of clay- to sand-size particles adversely affects reproduction in some groups, particularly the salmonids. This results from reducing the flow of water and, hence, the renewal of oxygen and removal of metabolic wastes from deposited eggs. Habitat modification, particularly the loss of cover for juvenile fish, and removal of suitable spawning sites may reduce certain fish populations. Other groups appear to be well adapted to turbid conditions and may replace more desirable species. In addition, sediment may affect fish production by regulating primary and secondary production or by limiting the accessibility of food organisms.

9.5.2 Sediment Impact by Regions

A survey of the distribution of sediment related research suggests that studies are concentrated in areas with economically important aquatic resources and specific environmental problems. Provinces receiving intensive study include Laurentian Mixed Forest, Eastern Deciduous Forest, Prairie Parkland, Rocky Mountain Forest, Willamette-Puget Forest, and Pacific Forest. In the Laurentian Mixed Forest region there is an emphasis on studies on the Great Lakes, especially in terms of sediment toxicity, effects of taconite tailings, the effect of turbidity on primary production, and the impact of sediments on salmonid fisheries. The relatively large number of studies in the Eastern Deciduous Forest Province can be attributed to the large area involved, as well as to concern with extensive development in terms of agriculture, forestry, mining, and construction. Research in the Prairie Parkland region developed from concern over limitation of primary production by clay suspensions and the resulting decline in fish yield in numerous farm ponds and reservoirs.

Several studies were located in the Rocky Mountain Forest province. Most of these considered the effects of development (impoundment, mining, construction) on benthos and fish. Studies in the Pacific Forest and Willamette-Puget Forest provinces considered the effect of sediment produced from logging, mining, or impoundment on existing salmonid fisheries and potential food organisms. Few studies were found in areas with low relief or low runoff. These areas include the Outer Coastal Plain Forest and 14 western provinces [California Parkland (2610), Great Plains Short Grass Prairie (3110), Palouse Grassland (3120), Intermountain Sagebrush (3130), Mexican Highlands Shrub Steppe (3140), Chihuahuan Desert (3210), American Desert (3220), Sierran Forest (M2610), California Chaparral (M2620), Upper Gila Mountains Forest (M3120), Colorado Plateau (P3130), and the Wyoming Basin (A3140)].

Water related problems in the 14 western regions are similar since precipitation is low in many areas and existing surface waters are extensively regulated by inter- and intra-state agreements. Extensive management and diversion of existing surface waters across regional boundaries for domestic, industrial, agricultural, and energy uses often conflict with the needs of aquatic biota. An assessment of the extent of aquatic research in these regions must acknowledge that institutional arrangements dictate that, in certain areas, aquatic biota are of secondary importance to more pressing demands.

9.5.3 Management of Sediment Impacts

The preferred approach to management of sediment impacts on biota is to prevent high sediment losses from watersheds to the water. Surface erosion may be reduced by maintenance of vegetated watersheds and river banks.

Disturbances to the watershed should be minimal and timed to occur during periods of low flow since most impacts by sediment are associated with snow melt or storm events. Since sediment carries nutrients, the time of sediment addition to water also may be a crucial factor in stimulating eutrophication.

Controlling existing sediment impacts may be best accomplished by using mitigating structures which provide habitats and reduce abrasion and scour by bed load sediment. High suspended sediment levels may require precipitation by chemicals.

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CHAPTER 10

THE ROLE OF PHOSPHORUS AND NITROGEN IN FRESHWATER ECOSYSTEMS AND THEIR IMPACT ON BIOTA

10.1 INTRODUCTION

Interest in the role of nutrients in influencing aquatic metabolism has been stimulated recently because nutrients have been implicated in accelerating eutrophication in many freshwater systems. Eutrophication is a natural aging process, whereby lake or stream basins gradually fill in, blooms of undesirable algae appear, and discoloration or loss of oxygen from the water with associated fish kills are observed. Man's urban, industrial, and agricultural activities result in increased nutrient loading and often accelerate the natural eutrophication process.

Two of the most important nutrients affecting aquatic metabolism are phosphorus and nitrogen. Phosphorus is involved in many cellular processes and is a critical component in basic metabolic reactions. Phosphorus has received considerable attention in freshwater ecosystems since it is often the least abundant of the major nutrients required in biological metabolism (Vollenweider 1968; Edmondson 1972; Schindler 1977). Therefore, levels of phosphorus frequently regulate primary productivity and additions of it to water bodies often are responsible for declining water quality. Nitrogen limits productivity in some systems and may become limiting seasonally in others. Organisms need nitrogen for building structural components, as an energy source, and for synthesizing proteins and pigments. Nitrogen is especially important to bacterial breakdown of detritus. Since species have individual nutrient needs, the levels of nitrogen and phosphorus are important in determining the species composition and the succession rate of a system.

In this chapter the impact of nutrients on biota has been examined by considering both the internal cycling and the result of external nutrient addition to various system types. Concentrations of various nutrient forms and the mechanisms of exchange between them are presented since the initial nutrient levels and rates of transformation determine system response to additional nutrient input. Cultural activities enhance nutrient additions to aquatic systems; therefore, the effect of these additions has been explored by considering studies of external loading of nutrients to water bodies. Lakes, streams, and reservoirs are all considered, since biotic response to nutrient addition may depend on system type. Methods for predicting biotic response are examined and suggestions for management made.

10.1.1 Forms and Distribution of Nutrients

Phosphorus

Phosphorus can be found in dissolved, colloidal, or particulate form, where it often is sorbed to other particles; it occurs as inorganic orthophosphate, polyphosphate, or as organic phosphorus (Kramer et al. 1972). Chemical analyses are based upon the reactivity of phosphorus with molybdate to form molybdophosphoric acid. Of the eight forms of phosphorus recognized, five have been widely used (Strickland and Parsons 1965). These forms are based on particle size, acid digestion, and reactivity with molybdate. Compounds requiring digestion with an oxidizing acid solution after membrane filtration (0.45 μ) are termed soluble phosphorus (SP). Compounds which react spontaneously with molybdate after filtration are designated soluble reactive phosphorus (SRP). Soluble unreactive phosphorus (SUP) is the difference between SP and SRP and is often referred to as organic phosphorus, although it is unclear whether all SUP compounds are, in fact, organic in nature. Total phosphorus (TP) is measured after acid digestion of unfiltered water with a strong oxidant such as potassium persulfate or perchloric acid. The total phosphorus minus the soluble phosphorus is termed particulate phosphorus (PP). The other three phosphorus fractions are subdivisions of the previously mentioned fractions. However, these are not operationally defined since they are not easily quantified. Particulate phosphorus is subdivided into reactive PP and inorganic and organic unreactive PP, while the components of SP consist of enzyme hydrolyzable phosphate and polyphosphates.

In many lakes, total organic phosphorus comprises up to 95 percent of the total phosphorus. However, orthophosphate phosphorus (PO_4-P or soluble inorganic phosphate) is probably the only form of phosphorus directly available to algae. This fraction, considered part of the SRP fraction, constitutes less than five percent of the total phosphorus found in temperate lakes. The PO_4-P pool turns over very rapidly and may be less than 0.02 mg/l in phosphorus-limiting waters (Rigler 1966). During summer, the turnover time (the time required to replace the phosphorus within a compartment) of PO_4-P in the epilimnion is generally between one and eight minutes, regardless of the trophic state of the water body (Rigler 1978). The SRP fraction has been found to be an overestimate of PO_4-P in many instances (Rigler 1966; Chamberlain and Shapiro 1969; Peters 1977). Only a small percent of the chemically determined SRP fraction may be PO_4-P, as was shown in Kuenzler and Ketchum (1962). Errors in determining the PO_4-P content of lakes may result from orthophosphate or organic phosphorus being released from ruptured cells during filtration, from organic phosphorus being hydrolyzed to PO_4-P during acidification, or from interferences with arsenate or germanium (Rigler 1966). However, the SRP-PO_4-P discrepancy may only be significant when phosphorus is limiting (Rigler 1973).

The supply of and demand for phosphorus will vary from lake to lake and from organism to organism. The average range of total phosphorus levels in lentic and lotic freshwaters of the United States is from 0.1 to 0.2 mg/l (Macgregor and Keeney 1975). Lakes exhibit standing total P concentrations ranging from 0.005 - 0.030 mg/l in summer to 0.008 to 0.08 in winter. Total P concentration in United States' rivers may range from 0.002 to 5.04 mg/l, with industrial loading increasing this value (Sanders 1972). For the Great Lakes, total P was found to be lowest in Lake Superior with a concentration of 0.005 mg/l and highest in Lake Ontario at 0.08 mg/l (Vollenweider 1968).

The amount of phosphate needed for optimal growth for phytoplankton will vary among individual species (Kuhl 1974), depending upon the amount of phosphorus available and the algal capacity for storing phosphorus. The phosphorus incorporated into algal cells can occur as polyphosphates, which can be accumulated and used when needed. This storage of an element in excess of normal metabolic requirements is known as luxury consumption (Hutchinson 1975). It is not known if luxury consumption occurs in all algae, but upper limits of phosphate tolerance for various algae have been found through culture experiments. The reason for phosphorus inhibition of growth in cultures is not clear (Rodhe 1948); however, it is rarely observed in situ (Fogg 1973). Phosphates have seldom been found in sufficient concentration to exhibit toxic effects upon higher organisms (McKee and Wolf 1971).

Nitrogen

The most biologically important inorganic forms of nitrogen in freshwater are ammonium (NH_4-N), nitrate (NO_3-N), nitrate (NO_2-N), and molecular nitrogen (N_2-N). Organic nitrogen occurs in particulate form (PON) as living organisms and detritus and in dissolved from (DON) in compounds such as amino acids, amines, polypeptides, humic acids, purines, pyrimidines, porphorines, vitamins, and urea. Separation of PON from DON is usually accomplished by retention on a 0.45 μ filter (Isirimah 1972).

Nitrogen concentrations in lakes vary with season and depth. Generally epilimnetic nitrogen concentrations are NH_4-N from 0-5 mg/l; NO_2-N from 0-0.1 mg/l; NO_3-N from 0-4 mg/l; DON from detectable to a few mg/l (Keeney 1973). In most deep temperate lakes minimum concentrations of epilimnetic organic nitrogen are found before overturn, with a sharp increase in concentration afterward. Nitrate is usually more abundant than ammonia, and nitrite is scarce or absent in waters that are well oxygenated. However, both nitrite and ammonia levels can be high in very productive water where reduced conditions are frequently encountered. In the anaerobic hypolimnion of lakes and in the interstitial sediment water, levels of ammonium can be above 10 mg/l and nitrite can range up to 1 mg/l (Hutchinson 1957; Konrad et al. 1970). Softwater lake sediments contained about twice the total N concentrations of hardwater lakes in Wisconsin (Keeney et al. 1970). Most of the nitrogen in lake sediments is organic (Keeney et al. 1970).

Streams are not as stable chemically as are lakes. They have more temporal variations associated with changes in river flow (Livingstone 1963). Total N concentration of United States rivers varies between 1 and 54 mg/l (Sanders 1972). Most of the inorganic nitrogen is oxidized and in the form of NO_3-N (Keeney 1976). The mean NO_3-N concentration of North American river water has been reported as being near 1 mg/l (Livingstone 1963; Golterman 1975).

DON often comprises over 50 percent of the total soluble nitrogen in freshwater, and probably much of the DON is in the form of amino nitrogen compounds (Peterson et al. 1925; Birge and Juday 1926; Hutchinson 1957;

Manny 1972; Macgregor and Keeney 1975). DON of both lakes and streams is often greater than PON, except under more eutrophic conditions when the pools may be equal (Peterson et al. 1925; Hutchinson 1957). Seasonal distribution of DON appears to be largely unpredictable and different for individual lakes (Lueschow et al. 1970; Manny 1972).

The optimal inorganic nitrogen concentration of planktonic diatom cultures is below 1 mg N/l and for green and blue-green algae is above 1 mg N/l (Vollenweider 1968). Due to luxury consumption, the nitrogen uptake may exceed the minimal concentration necessary for growth.

Several nitrogen forms can be toxic to higher biota. In most water the NH_4-N form of ammonia predominates; however, in very alkaline or warm water the NH_3-N form increases [Environmental Protection Agency (EPA) 1976]. The toxicity of ammonia to fish and invertebrates is a result of the NH_3-N fraction which is 50 times more toxic than NH_4-N (Tabata 1962). The Environmental Protection Agency (1976) has set the criterion for maximum permissible levels of NH_3-N in freshwater at 0.02 mg/l. The toxicity of nitrite to fishes varies according to species and size (Russo and Thurston 1976). Sensitive species may be killed by acute exposure as low as 1 mg NO_2-N/l (Russo et al. 1974; Smith and Williams 1974; Westlin 1974; Russo and Thurston 1975). Chronic exposure to lower concentrations may be toxic to some species or to fry which may be more sensitive [Sprague 1971; National Academy of Science (NAS) 1978]. The criterion of 10 mg/l NO_3-N is based on the hazard to warm-blooded organisms when high nitrate intake and subsequent reduction to nitrite impair hemoglobin transport of oxygen (EPA 1976).

10.1.2 Transformations of Phosphorus

The transformations of phosphorus involve biological and chemical constituents. Phosphorus assimilation and excretion by biota account for much of the recycling of phosphorus between its various forms. Chemical transformation occurs mainly through phosphorus complexing with other elements. A clearer understanding of phosphorus movement between its important forms has been obtained through the use of tracer studies. These studies generally employ compartmental analysis. The number of compartments in lakes or streams can be extremely large and are usually combined into operationally defined compartments. Much of the previous work on phosphate uptake measurements indicated that only two pools, soluble inorganic phosphorus and particulate phosphorus were important, with particulate phosphorus containing greater than 95 percent of the total phosphorus. However, two other fractions may contribute significantly to the inorganic phosphate pool (Lean 1973a, 1973b). These are a low molecular weight, organic compound (designated XP) derived from the particulate fraction, and a high molecular weight compound, actually a very small particulate form (Paerl and Lean 1976), referred to as colloidal phosphorus. Both of these fractions are potentially available for phosphorus uptake by plankton through the release of phosphate to the soluble inorganic fraction. The majority of the phosphorus is found in the particulate phase if all compartments are equally labelled (Fig. 10.1). Complete labelling of all compartments does not always occur. Rate constants, represented by $\underline{k}$ have been determined for several phosphorus exchanges (Lean 1973a) with $\overline{k_1}$, the uptake of PO_4, occurring most rapidly (0.9 relative mass units/min).

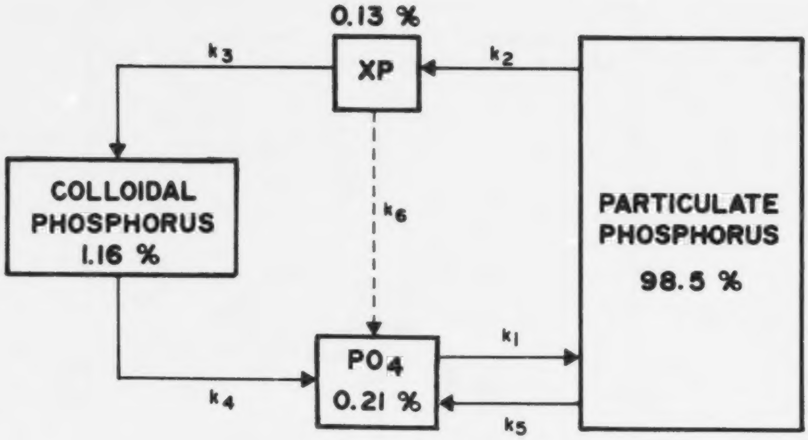

Fig. 10.1. Relative amounts of available phosphorus in the four principal compartments and exchange processes within the epilimnion. The k's represent rate constants. (From Lean 1973a.)

Figure 10.2 is a model of phosphorus cycling in the epilimnion of a eutrophic lake during summer (Rigler 1973). The arrows demonstrate the major phosphorus fluxes while the thickness of the arrow denotes the importance of the phosphorus exchanges. However, no rate constants are given. The model describes PO_4-P interactions and other components including the SUP pool represented by B and emphasizes the overall importance of the rapid turnover of PO_4-P. The phytoplankton are divided into two size classes to illustrate their relative roles in the rate of cycling of PO_4-P. A similar model describing phosphorus flows in a shallow, polluted river showed that PO_4-P was the major form assimilated by biota (Aiba and Ohtake 1977).

In most situations, a constant flux of phosphorus exists where organisms incorporate phosphorus and release it to the system through excretion and decay (Confer 1972; Kramer et al. 1972). The direct release of inorganic phosphorus compounds by ultraplankton, excretion by zooplankton, and enzymatic hydrolysis of organic material are postulated as three mechanisms which return PO_4-P to solution (Rigler 1973).

The cycling of phosphorus in the water is of extreme importance since it constitutes a main source of available phosphorus for biota. Primary producers, bacteria, and zooplankton are the major biotic cyclers, while complexing and dissociation are chemical mechanisms regulating phosphorus flows.

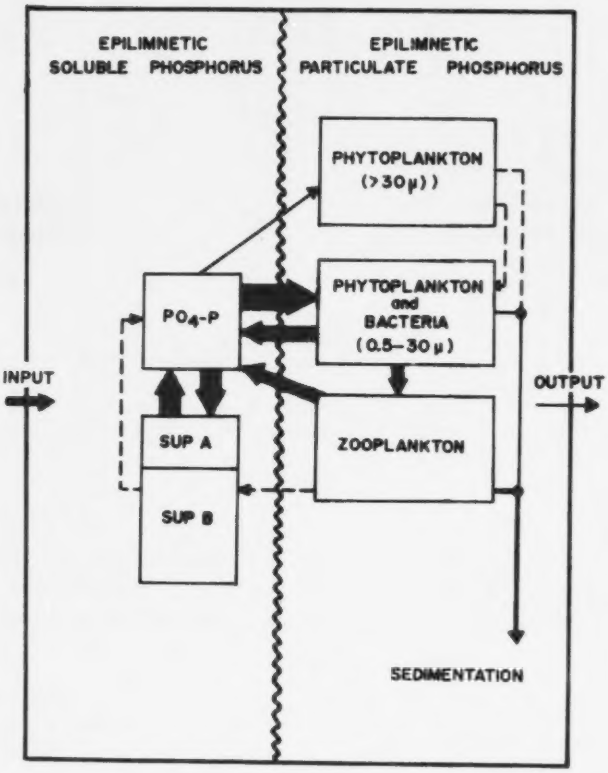
EPILIMNETIC SOLUBLE PHOSPHORUS
EPILIMNETIC PARTICULATE PHOSPHORUS
PHYTOPLANKTON (>30μ))
PHYTOPLANKTON and BACTERIA (0.5–30μ)
PO_4-P
INPUT
OUTPUT
SUP A
SUP B
ZOOPLANKTON
SEDIMENTATION

Fig. 10.2. The phosphorus cycle in a eutrophic lake indicating the importance of soluble PO_4-P and the exchanges occurring among compartments. Letters A and B represent soluble phosphorus other than PO_4-P. The least significant flows are dotted while the most significant flows are thickest. (From Rigler 1973.)

Algae

Assimilation of phosphorus by algae may vary by species and has been studied in relation to their growth (Fuhs and Canelli 1970). The growth kinetics of algae cannot be predicted from the amount of PO_4-P in water (Rhee 1972), since the concentration gives no indication of turnover rate. Even at high phosphate levels, cells take up and release phosphorus rapidly, although a lag phase often is seen before rapid growth begins (Lean and Nalewajko 1976). However, the rate of assimilation may depend on the concentration of PO_4-P in the water and thus be described by the Michaelis-Menten equation (discussed in the nitrogen assimilation section). An organism's ability to attach to surfaces, its sinking velocity, and its surface area to volume ratio are also significant factors affecting phosphorus uptake (Fuhs et al. 1972). Other factors such as pH (Schumacher and Whitford 1965; Viner 1975; Steeman-Nielsen and Rochon 1976), light (Kalff and Welch 1974; Jensen et al. 1976), temperature (McCombie 1960), or water velocity (Fogg 1973; Jensen et al. 1976) also may influence phosphate assimilation by algae.

Macrophytes

Phosphorus uptake in macrophytes has been studied mainly with regard to their ability to remove phosphorus from sediments and translocate it through their foliage (Bristow and Whitcombe 1971). Macrophytes also can remove phosphorus from the water. Whether the nutrient source is obtained mainly from the sedimens or water column depends upon the species and the relative concentration of phosphorus in the two compartments (Bristow 1974).

Bacteria

Bacteria absorb phosphorus as orthophosphate and excrete it in an organic form that may not be immediately available to algae (Phillips 1964). The rapid uptake of phosphorus by bacteria may be the primary reason that phosphorus turnover in lakes occurs rapidly. Within 20 minutes planktonic bacteria are capable of absorbing 95 percent of ^{32}P added to lake water (Rigler 1956). The competition for phosphorus by bacteria may retard algal growth, but bacterial growth may not be adversely affected to a great extent by algae (Rhee 1972). Release of organic phosphorus by bacteria has not been found to correlate with their growth rate or population size. Rapidly growing populations and those approximating steady state conditions both have been found to release significant amounts of dissolved organic phosphorus (Barsdate and Pretki 1974).

Zooplankton

Zooplankton act as rapid cyclers of phosphorus through microplankton grazing and fecal pellet production. Of the total amount of phosphorus ingested in the consumption of algae by zooplankters, approximately half is released as orthophosphate while the rest is excreted in feces. Since this grazing accounts for 12.6 percent of the total P removed from the trophogenic zone, whereas sedimentation only amounts to about 2 percent, the fecal material from zooplankton has presumably remained in the trophogenic zone where it can be consumed as detritus (Peters and Rigler 1973). In laboratory studies, the rate of phosphorus excretion from zooplankton was one-third to two-thirds less in the presence of bacteria. Phosphorus excretion by crustaceans and rotifers under certain conditions may be equal to the daily phosphorus requirement of phytoplankton (Hargrave and Geen 1968). The amount of phosphorus excreted daily by zooplankton may be nearly equivalent to their body weight of phosphorus. These zooplankton excretion products, mainly orthophosphate, can be incorporated and utilized by other biota (Peters and Lean 1973). Algal production can be regulated by zooplankton grazing and the rate of regeneration of PO_4-P in the water (Rigler 1974). Other factors considered to have an effect upon phosphorus release from zooplankton include: temperature, food supply (Butler et al. 1969), the size of zooplankton (Barlow and Bishop 1965), and detritus levels (Ferrante 1976).

Phosphorus Complexes

The complexing of phosphorus with metal ions in the open water depends on the amount and type of phosphates and metals present, the pH, and the presence of organic species, sulfates, and carbonates. Metal ions that complex and that may have a significant influence on phosphorus forms and distribution include ferric iron, manganese, zinc, copper, and aluminum. Humic and fulvic acids found in bogs and lakes also can form colloidal aggregates with iron and phosphorus (Shapiro 1964). With phosphorus addition to a fulvic acid-metal complex, fulvic acid is displaced from the metal and then reacts with the phosphate. When the metal is absent, no reaction occurs between phosphorus and fulvic acid (Levesque and Schnitzer 1967). Iron compounds differ in their affinity for phosphorus based on the oxidation state of iron and the presence of particulate organic matter (Koenings and Hooper 1976). Ferric oxyhydroxide complexes or nonreactive ferric iron are more effective at binding phosphorus than is a ferric colloidal complex (reactive ferric iron).

10.1.3 Transformations of Nitrogen

Figure 10.3 diagrams the important nitrogen transformations to be discussed:

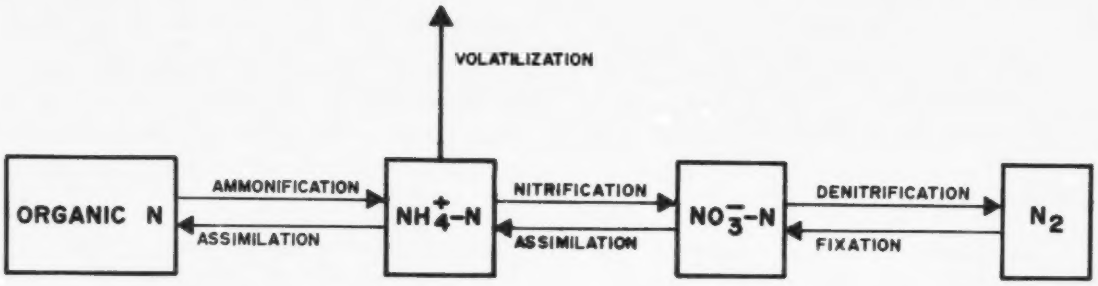

Fig. 10.3. Simplified biotic and abiotic nitrogen transformations. (Modified from Brezonik 1973 and NAS 1978.)

Assimilation

Assimilation is the incorporation of ammonium, nitrate, or organic nitrogen into living biomass (incorporation of molecular N_2 will be discussed as fixation). Most phytoplankton can use NH_4-N, or NO_2-N for the synthesis of cellular materials, but ammonium is reported to be preferred by most species (Syrett 1962; Brezonik 1972; Caperon and Meyer 1972; McCarthy et al. 1977). Use of reduced forms requires less energy expenditure. Energy is required both to reduce oxidized forms and to induce special enzyme systems for assimilation of the more oxidized forms (Eppley et al. 1969). When nitrogen is limiting, phytoplankton use all forms (NH_4, urea, NO_3, NO_2) in proportion to their availability (Dugdale and Dugdale 1965; McCarthy et al. 1977).

Laboratory culture experiments, although not necessarily representative of in situ conditions, indicate nitrate as an important nitrogen source for plankton (Chu 1943; Eppley et al. 1969). Optimal phytoplankton growth occurs when NO_3-N ranges from 0.9 to 3.5 mg/l. Below 0.1 mg NO_3-N/l nitrate can be limiting and the formation of chlorophyll may be inhibited. The upper limiting level or range is between 8.9 and 17.8 mg NO_3-N/l, depending on the species, and is 17.8 mg NH_4-N/l for all species studied (Chu 1943).

Some algae and macrophytes also can use dissolved organic nitrogen as a nitrogen source (Lund 1965; Wright and Hobbie 1965; Dugdale and Goering 1967; McCarthy 1972; North 1975). Bacteria generally utilize organic nitrogen substrates the most; less than 10 percent of organic nitrogen substrates in low concentrations are taken up by algae (Wright and Hobbie 1965). However, some phytoplankton possess permease systems similar to those of bacteria and are capable of active transport of dissolved organic matter (Shrift 1966; Hellebust and Guillard 1967; North and Stephens 1967; Hellebust 1970).

Sediments contribute nutrients to water since many transformations occur there. Benthic algae and bacteria also may directly assimilate sediment nutrients. Sediments also are prime nutrient sources for aquatic macrophytes, especially when nitrogen levels are low in the water (Nichols and Keeney 1976).

The rate of assimilation of nitrogen can be described by the Michaelis-Menten expression for enzyme kinetics:

$$v = \frac{V_m S}{K_s + S}$$

where v is the uptake rate, V_m is the maximum uptake rate, S is nutrient concentration, and K_s, the half-saturation constant, is related to the uptake mechanism (Eppley et al. 1969; Eppley and Thomas 1969; Caperon and Meyer 1972; Toetz 1973). Thus, at intermediate nitrogen concentrations, assimilation is proportional to nitrogen concentrations. Plants concentrate nitrogen by rapid uptake when levels are low and incorporate proportionately less when ambient concentrations are high.

The K_s of individual species is considered to be ecologically significant. Variations in growth rates and nutrient assimilation at different nutrient concentrations are important characteristics of species that may determine their geographic and seasonal distribution (Eppley and Thomas 1969; Eppley et al. 1969). Phytoplankton in oligotrophic systems have a lower K_s than those in a more eutrophic system (MacIssac and Dugdale 1969). Oligotrophic populations adapted to low nutrient concentrations are able to take up nutrients at a faster rate than species characteristic of a more eutrophic system (Carpenter and Guillard 1970). Competition for available nutrients at low concentrations may result in the evolution of species with a low K_s value (Toetz et al. 1977). Having a lower K_s value might allow a species to compete with a dominant species with a higher maximum growth rate (Dugdale and Goering 1967). The possession of different K_s and V_{max} values for different nutrients is an important factor in determining species domination or coexistance at varying levels of nutrients (Tillman 1977).

Other factors influencing assimilation are different regimes of nutrient preconditioning (Caperon and Meyer 1972); light, needed for assimilation of the less reduced nitrogen species (Toetz 1971, 1976); and the intracellular ratio of $[O_2]/[CO_2]$, which, when low, can induce the activation of enzymes for the reduction of oxidized nitrogen forms (Solomonson and Spehar 1977).

Ammonification

Ammonification is the decomposition of organic matter to ammonium by heterotrophic bacteria. Ammonification occurs simultaneously with assimilation, with the net difference between the transformations being reflected in the biomass level of nitrogen at a given time (Keeney 1976). Allochthonous and autochthonous sources of organic matter are decomposed in both the water column and sediments. The extent to which ammonification occurs in the sediments or in the water column depends on oxygen availability (Kleerekoper 1953).

In many aquatic systems regeneration by biota of inorganic and organic nitrogen (which is subject to ammonification) are significant processes. Many algae have been reported to excrete or release nitrogenous products which may be available to other organisms (Lund 1965; Wetzel 1969; Wetzel and Manny 1972; Hellebust 1978). Macrophyte pumping of nutrients from sediments with subsequent release to the water also increases nutrient availability (Toetz 1973, 1974; Nichols and Keeney 1976). Zooplankton also are major producers of regenerated organic nitrogen (Corner et al. 1965; Johannes 1968; Pomeroy 1970). Some systems may support large numbers of bottom-feeding fish which excrete significant levels of ammonium (Lamarra 1975a, 1975b). Other workers consider bacteria to be most important in nutrient cycling in water (Golterman 1960, 1964; Kuznetzov 1968; McCoy and Sarles 1969), although their role in converting organic nitrogen to more available forms is not well understood (Keeney 1973). At low nutrient concentrations they compete with other organisms and reduce the nutrients available to the rest of the system. However, under eutrophic conditions, bacteria may be very important in the breakdown of organic compounds to inorganic nutrients.

The ammonium content of sediments represents a large nitrogen pool potentially available to biota. The highest ammonium concentrations are associated with enriched sediments or with high organic loading (Brezonik 1973). The formation of ammonium in sediments is greatest at least 10 cm below the water-sediment interface (Serruya 1974.) The interface is the site of release of ammonium to the water column so that lower concentrations are seen in the upper sediments (Isirimah et al. 1976). The reduction of external nutrient loading can be insufficient to improve water quality due to nutrient regeneration from sediments (Gibbon 1971). Some sediments tend to sorb system (Carpenter and Guillard 1970). Competition for available nutrients at low concentrations may result in the evolution of species with a low K_s value (Toetz et al. 1977). Having a lower K_s value might allow a species to compete with a dominant species with a higher maximum growth rate (Dugdale and Goering 1967). The possession of different K_s and V_{max} values for different nutrients is an important factor in determining species domination or coexistance at varying levels of nutrients (Tillman 1977).

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Quantification of ammonification in the nitrogen budget is difficult since assimilation occurs simultaneously. Ammonification generally exceeds uptake in studies where both processes have been measured (Alexander 1970; Hanison 1979; Toetz and Cole 1978). Additional ammonium may be provided by precipitation, streamflow, and sewage effluent. Presumably, excess NH_4 is deposited in the sediments.

Ammonium Volatilization

Volatilization of ammonium may be a significant nonbiological loss of nitrogen when temperatures are high and the pH greater than 7.5 (Isirimah 1972). An increase in alkalinity may be associated with high turbulence or with high rates of ammonification or photosynthesis in lakes or streams (Stratton 1968, 1969; Isirimah 1972). The significance of this loss for a variety of aquatic situations needs investigation.

Nitrification

Nitrification is the oxidation of ammonium to nitrate with hydroxylamine, nitrous oxide, and nitrite formed as intermediates (Focht and Verstraete 1977). Two steps are involved in nitrification; both steps are mediated primarily by autotrophic, obligately aerobic microorganisms (NAS 1978). Nitrosomonas and Nitrobacter are the primary organisms oxidizing ammonium to nitrate in a series of steps (Suzuki et al. 1974). These nitrifiers can grow heterotrophically on organic matter (Focht and Verstraete 1977; NAS 1978). Other microorganisms capable of nitrification are present in fewer numbers, are strickly autotrophic, and have narrower temperature and pH ranges for optimal growth (Focht and Verstraete 1977).

The rate-limiting step in nitrification is the conversion of ammonium to nitrate (Garland 1977). Nitrifying bacteria are mesophilic, preferring temperatures in the range of 1 - 37° C (optimal temperature ca. 30° C), and preferring a neutral or slightly alkaline environment (Frederick 1956; Alexander 1965; Keeney 1973).

Activity by nitrifiers decreases sharply below pH 7 (NAS 1978). Nitrification does not occur significantly in the softwater lakes of Wisconsin (Chen et al. 1972b). The unbuffered softwater sediments dropped in pH sufficiently to inhibit microbial transformations. The discovery of significant rates of ammonium oxidation in acid environments revealed the occurrence of heterotrophic nitrification by various bacteria and fungi (NAS 1978). Although the importance of heterotrophic nitrification is not known, it is generally believed that autotrophic nitrification is more significant (Alexander 1971; Keeney 1973; Isirimah et al. 1976). Although oxygen is required, nitrification will occur at oxygen concentrations as low as 0.3 mg/l. Oxygen concentration is not as important as the rate of oxygen diffusion into the system (Greenwood 1962). Nitrification occurs in the water column and in the sediments, depending upon oxygen availability. In shallow, well-mixed lakes, nitrification by benthic autotrophs may be important to organisms in the water column (Trifonova 1963). However, not all of the nitrate formed may be available to biota in the water, since nitrate can diffuse back to the sediments where it can be immobilized by benthos or denitrified (Chen et al. 1972b). Nitrification may not be as significant in the water column since nitrifiers are not successful competitors against phytoplankton for ammonium at concentrations below 0.1 mg NH_4-N/l (Goering 1972).

Nitrification is not an important process in streams containing less than 0.5 mg NH_3-N/l and which lack substrate for nitrifying organisms (Garland 1977). The majority of nitrifying bacteria are attached to plants or found within the top centimeter of sediments. Nitrification also is inhibited in grossly polluted streams which lack oxygen. Oxidation of ammonium is inversely related to flow since the amount of nitrate formed depends on the period of contact with the sediments.

In the presence of oxygen, nitrification is an important process in streams, converting much of the ammonium loading to nitrate. Nitrification in rivers can result in the conversion of half the ammonium loading to nitrate and may represent eight times the ammonium assimilated into biomass (Gujer 1978). However, nitrification creates a large oxygen demand in lakes and streams. To oxidize 1 mg of ammonia to nitrate requires more than 4 mg of oxygen (Montgomery and Borne 1966; Wezernak and Gannon 1967). In the River Trent, U.K., nitrification accounted for 75 percent of the total oxygen demand (Garland 1973).

The process of nitrification is most important in sediments of warm, shallow lakes and streams which are well-mixed, but the process also might be observed during turnover in deeper lakes. Although the length of time nitrification occurs in deep lakes may be short, rates of oxidation are rapid, and significant amounts of nitrate may be formed (Keeney 1973). The amount of nitrate available in the water column will depend on the rates of diffusion of nitrate back to the sediments and subsequent denitrification.

Denitrification

Denitrification, the reduction of nitrite or nitrate to N_2O and N_2, results in a loss of nitrogen from aquatic systems. The process occurs in water or in sediments when oxygen levels are low and where sufficient organic matter is present to act as an energy source (Broadbent and Clark 1965; Goering and Dugdale 1966; Brezonik and Lee 1968; Chen et al. 1972a; Koike et al. 1972; Keeney 1973; Anderson 1977; Tiren 1977). Decomposition of organic matter also consumes oxygen. When oxygen is depleted, bacteria use nitrate as a terminal electron acceptor, releasing a reduced form of nitrogen.

Nitrous oxide (N_2O) can be an intermediate product of denitrification and is the sole product of some bacteria (Focht and Verstraete 1977). Although N_2O is considered a minor product of denitrification, the proportion of N_2O increases below temperatures of 5° C and below pH values of 5 to 6 (Focht 1974; Stanford et al. 1975). Production of N_2O is of concern due to its role in destruction of stratospheric ozone (NAS 1978).

Facultative anaerobes such as Pseudomonas, Achromobacter, Bacillus, and Micrococcus are responsible for the reduction of nitrite and nitrate, but they also are capable of other nitrogen transformations such as ammonification (Alexander 1961) since the electron transport system of these facultative anaerobes is identical prior to the terminal enzymes under both aerobic and anaerobic conditions (Bandurski 1965). Denitrification does not require completely anoxic conditions but has been reported to occur at low oxygen levels (Koike et al. 1972; NAS 1978). Since the microorganisms are facultative they are able to withstand periodic aerobic conditions and may participate in denitrification in microanoxic zones.

The rate of denitrification is influenced not only by oxygen supply and available energy sources, but also by temperature, pH, trace minerals, and nitrate concentration. The temperature range for denitrification is from less than 5° C (Goering and Dugdale 1966) to 60° (Nommik 1956), although individual species have narrower ranges. Optimal temperatures are high, near 60° C (Nommik 1956; Bremmer and Shaw 1958). Denitrification is more important under neutral or alkaline conditions than under acid conditions, with an optimal pH from 7 to 8 (Nommik 1956; Bremmer and Shaw 1958; Chen et al. 1972a; Brezonik 1973). Small amounts of molybdenum are required as a component of the enzyme nitrate reductase. The rate of denitrification also increases with increased nitrate concentration (Koike et al. 1972).

Denitrification can be a significant loss of nitrogen in eutrophic lakes (Goering and Dugdale 1966; Brezonik and Lee 1968; Kuznetsov 1968; Chen et al. 1972c; Andersen 1974; Tiren 1977). The nitrogen loss can represent as much as 80 percent of the nitrogen loading, especially in shallow, polluted lakes (Vollenweider 1968; Ryding and Forsberg 1977). Transport of nitrate to anoxic sediments by groundwater seepage may result in nitrogen losses by denitrification (Keeney et al. 1971). Frequent changing from aerobic to anaerobic conditions may stimulate nitrogen losses from alternating nitrification and denitrification, as has been shown for soils (Reddy and Patrick 1976).

A difficulty encountered in quantifying rates of denitrification is separating denitrification from other simultaneously occurring transformations. Ammonification and nitrification are necessary for formation of sufficient concentrations of nitrate. However, nitrification proceeds most rapidly under aerobic mixed conditions, while denitrification requires anaerobic conditions. Assimilatory nitrate reduction also competes with denitrification (Brezonik and Lee 1968; Keeney et al. 1971; Isirimah et al. 1976). Generally aquatic sediments are an ideal site for denitrification, since levels of organic matter are high, and low oxygen conditions are frequently encountered. As long as sufficient nitrate is supplied, the denitrification process can be a major nitrogen loss.

Nitrogen Fixation

One major source of nitrogen in aquatic systems is fixation of molecular nitrogen in surface waters and sediments. In the eutrophic zone, fixation is associated with blue-green algae and photosynthetic bacteria. In deeper waters and in sediments, heterotrophic bacteria are responsible for fixation. Many genera of algae and bacteria are known nitrogen fixers and many others are believed to have this ability. NAS (1978) provides a summary of these species and their habitats. With the introduction of the acetylene reduction method by Stewart et al. (1967), in situ nitrogen fixation measurements are made frequently. However, several errors can be associated with the technique, and values reported may not be accurate (Rusness and Burris 1970; Horne and Viner 1971; Wong and Burris 1972; Mague and Burris 1973; Flett et al. 1975).

Autotrophic Fixation:

Most nitrogen fixing blue-green algae in freshwater are filamentous and have heterocysts. Nitrogenase, the enzyme associated with fixation, is located with the heterocysts (Fay et al. 1968) as a protection against high oxygen levels which inhibit nitrogenase activity and thus fixation (Lang and Fay 1971; Fogg et al. 1973; Paerl and Keller 1977; Paerl 1978). Fixation does occur in aerobic waters through the use of structural, chemical, and ecological adaptations of blue-greens.

Photosynthetic bacteria require anoxic conditions and light simultaneously so that their role in fixation is thought to be small (NAS 1978).

Occurrence and rates of fixation may depend on the availability of other nitrogen sources. High dissolved organic nitrogen levels have been correlated with high fixation rates, but this may be a noncausative relationship since high phytoplankton biomass would increase dissolved organic nitrogen (Horne and Fogg 1970; Fogg et al. 1973). Some dissolved inorganic nitrogen might be needed as a "starter" for fixation (Goering and Neess 1964; Horne et al. 1972). Fixation occurs in the presence of nitrate and ammonium, but rates may not be maximal until these nutrient concentrations are low, although low levels might represent high turnover. Nitrogen fixation may be more effectively inhibited by ammonium than by nitrate (Allen 1956; Toetz 1973). The use of inorganic nitrogen is preferred since fixation of molecular nitrogen requires a large energy input. Several investigators suggest that nitrogen fixation will occur regardless of ambient concentrations of inorganic nitrogen whenever nitrogen demand exceeds supply (Dugdale and Dugdale 1965; Billaud 1967, 1968; Horne et al. 1972).

Fixation also depends on available phosphorus. Phosphorus enrichment has been shown to stimulate nitrogen fixation (Toetz 1973; Lean et al. 1976). Other workers have reported high levels of phosphorus associated with nitrogen fixation (Tew 1959; Dugdale and Dugdale 1962; Granhall and Lundgren 1971; Horne 1971; Horne et al. 1972).

Levels of organic carbon may influence the amount of nitrogen fixed. Glucose has no consistent effect on nitrogen fixation in the dark but inhibits light fixation (Goering and Neess 1964). Since blue-green algae are facultative heterotrophs, they may switch from photosynthesis to the use of organic compounds as an energy source in the dark. However, heterotrophic fixation occurs at a slower rate (Virtanen and Miettinen 1963).

It has been suggested that blue-green algae become dominant when productivity levels are high since they are more efficient at obtaining carbon dioxide (CO_2) at low concentrations than green algae (King 1970; Shapiro 1973).

When CO_2 levels are low, the pH also is high. Therefore, the lowering of pH or the addition of CO_2 may result in a shift from blue-green to green algae. Simultaneous addition of nutrients hastens this process; however, nutrient addition alone stimulates blue-green algal growth.

Other nutrients required for fixation include: Ca, Mo, B, Fe, and Na (Tew 1959; Goering and Neess 1964; Fogg et al. 1973). Molybdenum and iron are essential components of the enzyme nitrogenase. The other nutrients listed are needed for growth on elemental nitrogen.

The availability of iron may be an important factor in determining the algal composition of an aquatic system. High rates of nitrogen fixation result in a large demand for iron (Lean et al. 1976). As iron becomes limiting, some blue-green algae may produce hydroxamate chelators which not only increase the availability of iron but also inhibit the growth of other algae (Murphy et al. 1976). The result is an algal community dominated almost entirely by blue-greens.

Important physical factors affecting nitrogen fixation are temperature and pH. Nitrogen fixation can occur over a wide range of temperatures (by different species), although it is usually observed at times of greatest water temperature in temperate, eutrophic lakes. However, other factors such as limited nitrogen availability may be more important than temperature in determining the occurrence of fixation (NAS 1978). Tolerance to a wide range of pH also is observed for nitrogen fixers as a group, although alkaline environments are preferred (NAS 1978).

There is some evidence for seasonal and spatial succession among blue-green nitrogen fixers. Aphanizomenon generally appears later in warm seasons than Anabaena (Granhall and Lundgren 1971) and may require higher levels of phosphorus (Vanderhoef et al. 1974). Aphanizomenon is found deeper in the water and uses reduced carbon rather than CO_2 (Fogg et al. 1973). Anabaena is the more efficient nitrogen-fixer, as it contains more heterocysts per strand (Granhall and Lundgren 1971). Many species, including these two, are believed to produce self-inhibitors which may be important in regulating blooms (Horne and Goldman 1972).

A study of blue-green algal succession in Green Bay, Lake Michigan, from the eutrophic mouth of the Fox River out to more oligotrophic lake water revealed that Microcystis (a non-fixer) dominated when concentrations of all nutrients were high (Vanderhoef et al. 1974). Aphanizomenon was found in moderately eutrophic areas and fixed nitrogen as long as phosphorus was available. As phosphorus levels declined, diatoms became dominant. In a lake with a distinct and stable nutrient gradient, as in this case, there are consistent variations in algal growth and in fixation rates. In other lakes, blooms may be distributed randomly and may be moved by lake currents, making fixation-rate calculations more difficult (Vanderhoef 1976).

The rates of fixation in lakes of varying trophic states have been compared. Fixation may be highest at intermediate levels of eutrophication due to the opposing effects of organic nitrogen and nitrate concentrations (Horne et al. 1972; Brezonik 1973). Nitrogen fixation in shallow, moderately eutrophic systems is important in the nitrogen budget and may represent up to 40 percent of the lake's yearly nitrogen loading (Granhall and Lundgren 1971; Horne and Goldman 1972; Torrey and Lee 1976). Oligotrophic lakes lack sufficient nutrients for fixation to be significant. When nutrients are low, diatoms outcompete blue-green algae to become the dominant phytoplankton (Welch et al. 1972; Keating 1978). In stratified, nonoligotrophic lakes, proper conditions for fixation are found at the end of the spring phytoplankton bloom and during the autumn overturn. Nonstratified, nonoligotrophic lakes may demonstrate irregular fixation as optimal conditions occur periodically (Horne et al. 1972).

Heterotrophic Fixation:

Optimal physical conditions for heterotrophic fixation are different from those for autotrophic fixation. Controversial evidence exists for fixation by yeasts and fungi, but bacterial fixation is well documented (Keirn and Brezonik 1971). The bacteria responsible are facultative anaerobes which are not sensitive to temperature, allowing fixation to occur over a longer season and at greater depths (Kerin and Brezonik 1971; Brezonik 1973; Whitney et al. 1975). They require anoxic conditions or may be found at the anaerobic-aerobic interface (Brezonik and Harper 1969; Keirn and Brezonik 1971; Brezonik 1973; Whitney et al. 1975). At least 18 genera of heterotrophic bacteria may be capable of nitrogen fixation (NAS 1978).

The main factor limiting bacterial fixation is a sufficient carbon energy source, since these bacteria are inefficient users of carbon and also must compete for available carbon with both fixers and nonfixers (Stewart 1969; Toetz 1972; Brezonik 1973; Whitney et al. 1975; Hanson 1977a, 1977b). Additions of sucrose, but not glucose, pyruvate or butyrate have been shown to stimulate nitrogen fixation in anoxic sediments (Keirn and Brezonik 1971). However, no relationship has been observed between nitrogen fixation and sediment ammonium, total organic nitrogen, phosphorus, percent volatile solids, or nitrogen (Brezonik 1973).

Bacterial fixation in deeper waters and sediments has not received much attention but may be a significant nitrogen source (Brezonik and Harper 1969; Keirn and Brezonik 1971; Brezonik 1973; Macgregor et al. 1973; Macgregor and Keeney 1973). However, nitrogen fixed in sediments may not be available to biota. Much of it may be denitrified. Although more research is needed to determine the significance of sediment fixation, it may be of minor quantitative importance in the nitrogen budget of most lakes. The importance of nitrogen fixing heterotrophs lies in their widespread distribution and ability to fix small quantities of nitrogen over prolonged periods of time.

10.1.4 Nutrient Budgets

Nutrient budgets which consider the internal levels of various forms and the rates of exchange between pools are useful in determining the impact of nutrient loading. Although a few whole lake budgets have been constructed, more are needed, especially for different system types and trophic states. Few phosphorus budgets exist because methods of distinguishing between all forms are not reliable, turnover between forms is rapid, and concentrations are low. Mass balance nitrogen budgets for a few lakes have been summarized by NAS (1978). These budgets consider internal pools and fluxes as well as external nitrogen sources and losses from fixation and denitrification. Although the transformations of nitrogen are known, how pool size and rates of transformations vary from system to system needs more attention. Since some nitrogen transformations increase, paralleling eutrophication, these exchange rates can be important predictors of system behavior. Much of the information obtained from nutrient budgets can be used to develop models predicting system behavior (see section 10.3.1).

10.2 THE IMPACT OF NUTRIENTS ON BIOTA

10.2.1 Biotic Level of Impact

An increase in primary productivity or a shift in the dominant producer species usually occurs following nutrient enrichment in systems such as lakes where productivity exceeds respiration ($P/R > 1$). However, productivity may be limited by factors other than nutrients. For example, in reservoirs productivity frequently is limited due to high turbidity (Silvey and Wyatt 1971), while in streams, producers may be restricted by dense canopy cover or by turbulent flow. Streams have been described as a continuum from heterotrophic headwaters to autotrophic middle stretches to heterotrophic mouths (Cummins 1975). Only in the heterotrophic reaches of nutrient poor streams can nutrients limit primary productivity. In the detrital based reaches of streams ($P/R < 1$) nutrients are not expected to augment primary production, although nitrogen addition may stimulate detrital breakdown, thereby stimulating primary or secondary productivity.

A systems's response to nutrient addition will depend upon the degree of impact. Nutrient input may stimulate productivity up to a certain level. Thereafter, increased additions no longer will affect the response, or a negative effect will be observed. This response gradient may be represented by a "performance curve," where response is plotted on the y-axis and increasing input is plotted on the x-axis (Odum et al. 1979). A series of performance curves may represent the succession of populations as nutrient input increases (Fig. 10.4).

The points at which these curves intersect reflect a shift in the major dominant group. The figure may represent a phytoplankton succession (i.e., diatoms to greens to blue-greens), a succession of macrophytes (i.e., submerged to floating to emergent), or a successional series of higher organisms such as fish (i.e., trout to bass to carp).

Although the successional changes are correlated with increased nutrient concentrations, the impact of nutrients often is indirect. Even at the phytoplankton level, community shifts may not be directly related to nutrient additions. For instance, blue-green algae may become dominant at low CO_2 concentrations, which result from increased productivity, although this increase in productivity is caused by nutrients initially.

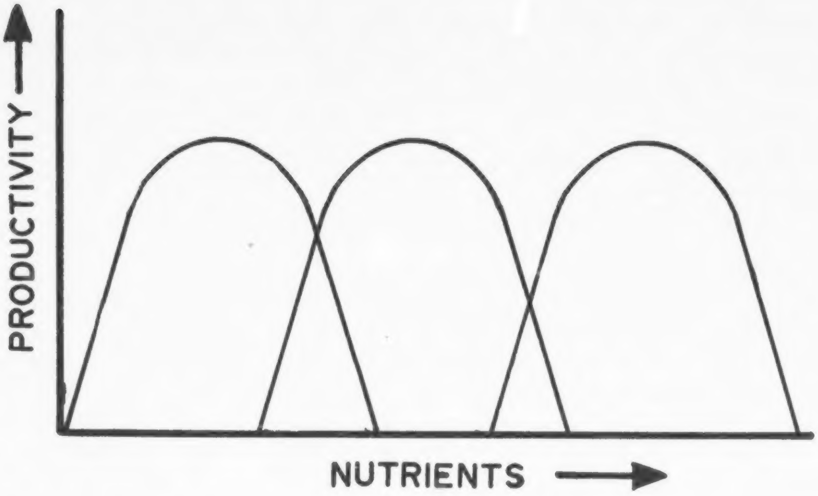

Fig. 10.4. Succession of populations as eutrophication increases.

Since nutrient input does not directly affect higher organisms, responses of primary and secondary consumers often depend on the algal response or on microbial breakdown of detritus. Therefore, the degree to which the impact is propagated through the food web must be considered. A productivity pyramid for a low nutrient pond was estimated from the rate of phosphorus uptake (Whittaker 1975) although this transfer of energy should apply to other system types and trophic states. Comparing assimilation between two trophic levels or comparing herbivore assimilation with gross primary productivity at the second level results in an "ecological efficiency of energy flow" (Whittaker 1975). Upon nutrient addition, the percent change in the lowest trophic level will be comparable to the percent change observed in productivity at each of the higher levels as long as species composition remains constant. Therefore, if primary productivity is increased by 5 percent, herbivore and carnivore productivities also may each increase by 5 percent. This supports the observation that slight increases in productivity often stimulate an increase in zooplankton numbers or in fish yield. However, this change in productivity may not be sustained through the food web if species composition changes or if the primary producers are inedible. In other instances organisms may not be participants in the same food web, but through a modification of the environment one species will influence another. In these cases the impact is more difficult to ascertain and estimate.

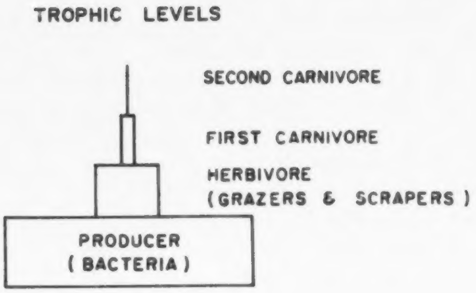

Fig. 10.5. Productivity pyramid for a low productivity pond. Trophic levels which apply for streams are indicated in parentheses. (Adapted from Whittaker 1975.)

10.2.2 Modifiers of Impact Response

Understanding the impact of nutrients in freshwater lakes and streams requires not only consideration of external factors modifying system behavior but also consideration of the internal state of the system. External factors, which include physical and chemical parameters influencing productivity and watershed activities, are examined first. Then internal factors are considered, including water properties influencing the trophic state, other biota present, nutrient ratios, and interactions with sediemnts.

External Physical and Chemical Controls

Spatial heterogeneity across the United States (climatic, geologic, hydrologic, biotic, etc.) create a wide range of conditions which influence the nature of water bodies and their responses to nutrient inputs. A consideration of the many variables impinging on an ecosystem makes each system unique. Some of the more important controls are enumerated in this section. However, a number of features, i.e., components and processes, are common to many freshwater ecosystems allowing an aggregation of systems into a hierarchical scheme.

Climatic variables have an overriding influence on system behavior. Temperature, for example, regulates organismal metabolism and affects species composition. Temperature extremes may control both seasonal and daily mixing. Increased temperature results in decreased oxygen solubility. The extent to which evaporation occurs and the amount of ice cover are regulated by temperature. Light levels and the amount of precipitation also are climatic variables. Major geologic formations and soil types in conjunction with climate determine the dominant vegetation and level of nutrient loading.

Watershed Activities

The type of watershed has a major influence on external loading rates and nutrient concentrations observed in the water. Nutrients may enter aquatic systems from natural or cultural sources. Natural nutrient sources include contributions such as precipitation, groundwater, and runoff associated with geology. Cultural sources include inputs from deforestation, agricultural practices, and urbanization, and from sewage and industrial effluents. Most phosphorus loading is associated with cultural activities, while the majority of nitrogen input may be from natural sources. For example, estimations of nutrient sources for Lake Mendota show that 60 to 70 percent of the phosphorus results from man's activities, and that the same percentage of nitrogen input is associated with natural sources (Lee 1969).

Data from several references considering inputs to lakes and streams have been compiled in Table 10.1. Based on the average values of several studies, deforestation and agricultural practices increase both nitrogen and phosphorus loading, although urban runoff contributes a significantly greater proportion of phosphorus. Precipitation can be an important phosphorus source and generally is a significant source of nitrogen. Groundwater also contributes significantly to the nitrogen pool, although it is difficult to manage.

Water Properties

A number of internal properties of freshwater systems influence nutrient and sediment impacts. Morphometric and hydrologic features will affect the extent to which nutrient loading can be tolerated, as well as determine the presence or absence of benthic producers. Important chemical factors regulating which biotic forms are present include pH, redox, organic matter, and the forms and concentrations of nutrients. Indigenous biota will control rates of nutrient cycling and the availability of nitrogen and phosphorus compounds.

Nutrient addition stimulates productivity to a greater or lesser degree dependent upon the site of addition. Injection of nutrients into the epilimnion may support a large crop of phytoplankton, since the nutrients are readily available. When injection is into the hypolimnion most of the nutrients are sedimented, and stratification reduces upward movement. However, in either situation, by fall turnover the majority of added nutrients may be unavailable.

Trophic States

Variations in concentrations of nutrient species are a result of differing levels of external input as well as varying internal biotic and abiotic cycling. Concentrations generally refer to the standing quantity of nutrients at a particular time. This information does not indicate the rate or amount of flux through the system nor the rate or amount of cycling within it. The concentrations of nutrients often are lowest at times of highest productivity due to high rates of flux. However, the mean annual standing quantities do

Table 10.1. Annual loading of nutrients. [Unmarked - nutrients enter per surface area of watershed (kg/ha-yr); * - nutrients in waters entering aquatic systems from watershed (Kg/yr); + - nutrients entering surface area of water body (kg/ha-lake surface-yr); average - average of nutrient entering per surface area of watershed (kg/hr-yr).]

Source	Total N	Total P	Reference
Forest Runoff	1.3-5.0	0.084-0.18	Cooper 1969
"	2.5		Keeney 1976
"	4.4	.083	Omernik 1976
"		.047 (Igneous)	Dillon & Kirchner 1975
"		.117 (Sedimentary)	Dillon & Kirchner 1975
"	2.5		Uttormark et al. 1976
"	0.198*	.019*	Macgregor & Keeney 1975
Average	3.14	0.102	
Forest and Pasture	1-5	0.15-0.75	Vollenweider 1968
"	2.5		Keeney 1976
"		.102 (Igneous)	Dillon & Kirchner 1975
"	5.5	.174	Omernik 1976
"		.233 (Sedimentary)	Dillon & Kirchner 1975
"	0.246*	0.164*	Macgregor & Keeney 1975
Average	4.67	0.28	
Agricultural	5		Uttormark et al. 1976
"	22.4	0.18	Montelaro 1970
"		.046	Dillon & Kirchner 1975
"	5		Keeney 1976
"	9.8	.308	Omernik 1976
Average	10.6	0.18	

Table 10.1. (Continued)

Source	Total N	Total P	Reference
Urban Runoff	8.8	1.1	Weibel et al. 1966
"		1.1-16.6	Dillon & Kirchner 1975
"	5		Uttormark et al. 1976
"	5		Keeney 1976
"	7.9	.301	Omernik 1976
"	2.010*	0.567*	Macgregor & Keeney 1975
		10-14400 ug/l	Sylvester 1961
Average	6.7	4.8	
Ground Water	15.600*	0.130*	Macgregor & Keeney 1975
Industrial	0.680*	0.046*	Macgregor & Keeney 1975
Septic Tanks	4*		Keeney 1976
Precipitation on Lakes	5.8+	0.44+	Brezonik et al. 1969
"	1.8-9.8+	0.15-0.6+	Vollenweider 1968
"	10-20		NAS 1978
"	15+		Keeney 1976
"		0.24-1.02+	Dillon & Rigler 1975
"	3.160*	0.071*	Macgregor & Keeney 1975
Average	8.1*	.49+	

give the relative abundances of nutrients and do help predict the kinds of organisms expected. Mean concentration values are used in estimating lake productivity which, in turn, will influence the response of the lake to nutrient loading. Table 6.5 in the chapter on impact assessment relates epilimnetic nutrient concentrations to lake productivity.

Nutrient Ratios

A biotic response is observed upon addition of a limiting factor to a system. In lakes, evidence suggests that the most important nutrient factors causing a shift from low to high productivity are phosphorus and nitrogen. The nitrogen to phosphorus ratio may indicate that one of these nutrients is limiting. Phosphorus may be limiting above an approximate N:P of 10:1 and nitrogen limiting below this level (Chiandani and Vighi 1974; Lambou et al. 1976). Lakes exhibiting ratios near 10 may show no response to single nutrient additions but often respond to additions of both. However, other nutrients or physical factors may be limiting in other systems.

The optimal N:P ratio is species specific and different species within a community may be limited by different nutrients simultaneously (Fitzgerald 1964; Rhee 1978). The comparison of the relative residence times of phosphorus and nitrogen will indicate which nutrient is in greater demand, with the nutrient that moves through the system faster being limiting (Vollenweider 1975).

In fast flowing detrital based systems nitrogen is the limiting factor for decomposition of organic matter. Nitrogen or phosphorus may be in short supply in autotrophic reaches, although both nutrients may be present in excess if these reaches are eutrophic.

Oligotrophic lakes may be limited by any of several nutrients or elements. However, since the metabolic demands of organisms require high nitrogen and phosphorus relative to minor nutrients, either of these elements is more likely to be limiting. In mesotrophic and moderately eutrophic lakes, phosphorus is often the limiting nutrient since nitrogen fixation can resupply nitrogen losses. Eutrophic lakes may be nitrogen- or phosphorus-limited, depending upon the amount of phosphorus released from sediments, rates of denitrification and nitrogen fixation, metabolic activity of biota, and the type of nutrient input to the lake. Marked nitrogen limitation was observed associated with point-source pollution even while the main portion of the water body was limited by phosphorus in large lakes and reservoirs examined by the National Eutrophication Survey (NES)(Allum et al. 1972). With increasing eutrophication, nitrogen metabolism often is speeded up more than phosphorus metabolism so that nitrogen may become the controlling factor (Vollenweider 1975). The transition from phosphorus- to nitrogen-limitation as eutrophication proceeds may result from increases in denitrification rates.

The nutrient limiting a system also may be related to organic carbon levels. Those systems which have a relative excess of carbon or are detrital based systems (i.e., headwaters of streams, hypereutrophic lakes, and estuaries) are more likely limited by nitrogen necessary for decomposition.

Lake productivity, on the other hand, is most frequently limited by phosphorus since algal carbon and nitrogen needs can be supplied from the atmosphere. Having different optimal nutrient requirements limits species to particular system types, trophic structures, or to a particular time in the seasonal succession.

Interaction of Sediments and Nutrients

Nutrients are accumulated in sediments over time and can be released in response to biological depletion of nutrients in the water column. It is well known that the sediments act as a net sink for phosphorus and nitrogen. Recently, however, the significance of sediments as a nutrient source has been debated. A conceptual model of sediment-nutrient interactions is given in Fig. 10.6. This figure illustrates the influence of suspended and bed load sediment on growth and reproduction of biota and indicates regulation of nutrient pools by sediments.

Sediment consists of organic and inorganic material produced by weathering of inorganic matter and from decomposition of organisms. The inorganic fraction consists of clay minerals, iron, and manganese oxides, carbonates, and the parent material from which these minerals are derived. The organic fraction consists of compounds ranging from simple amino acids through larger compounds such as chitin to complex compounds such as humic substances (humic and fulvic acids), as well as the remains of organisms such as bacteria, plankton, or cast exoskeletons.

Physical and chemical, as well as biological processes, are involved in nutrient transformations and exchanges between the sediments and water column are discussed in the following sections.

Physical and Chemical Processes of Nutrient Movement

Two chemical processes are involved in the movement of nutrients into and out of sediments. The process of adsorption-desorption can be a significant nutrient source or sink, depending on chemical conditions, while diffusion is a slower, bidirectional process relying on concentration differences. The accumulation of nutrients in sediments is a result of the physical process of sedimentation being greater than diffusion or mixing upward.

The phosphorus adsorbed onto sediments occurs mainly as apatite, organic compounds, and in complexed form with such ions as Fe, Ca, Mg, and Al (Taylor and Kuniski 1971; Williams et al. 1971; Emerson 1976). The reactive phosphorus, or that fraction potentially available to biota upon release from sediments, often is referred to as labile phosphorus and amounts to less than 5 to 10 percent of sediment total P (Taylor 1967).

Ammonia produced from organic decomposition will accumulate in sediment pore water. The extent to which ammonia is adsorbed depends on the amount of clay or other inorganic colloids present to bind it, and on the concentrations of other cations (Ca, Na, K, Mg) it might replace (Grim 1968; Armstrong and Chesters 1964; Bremmer et al. 1967; Toetz 1970). Adsorption is fast, but quantities absorbed may not be great (Brezonik and Fox 1976). When sediments

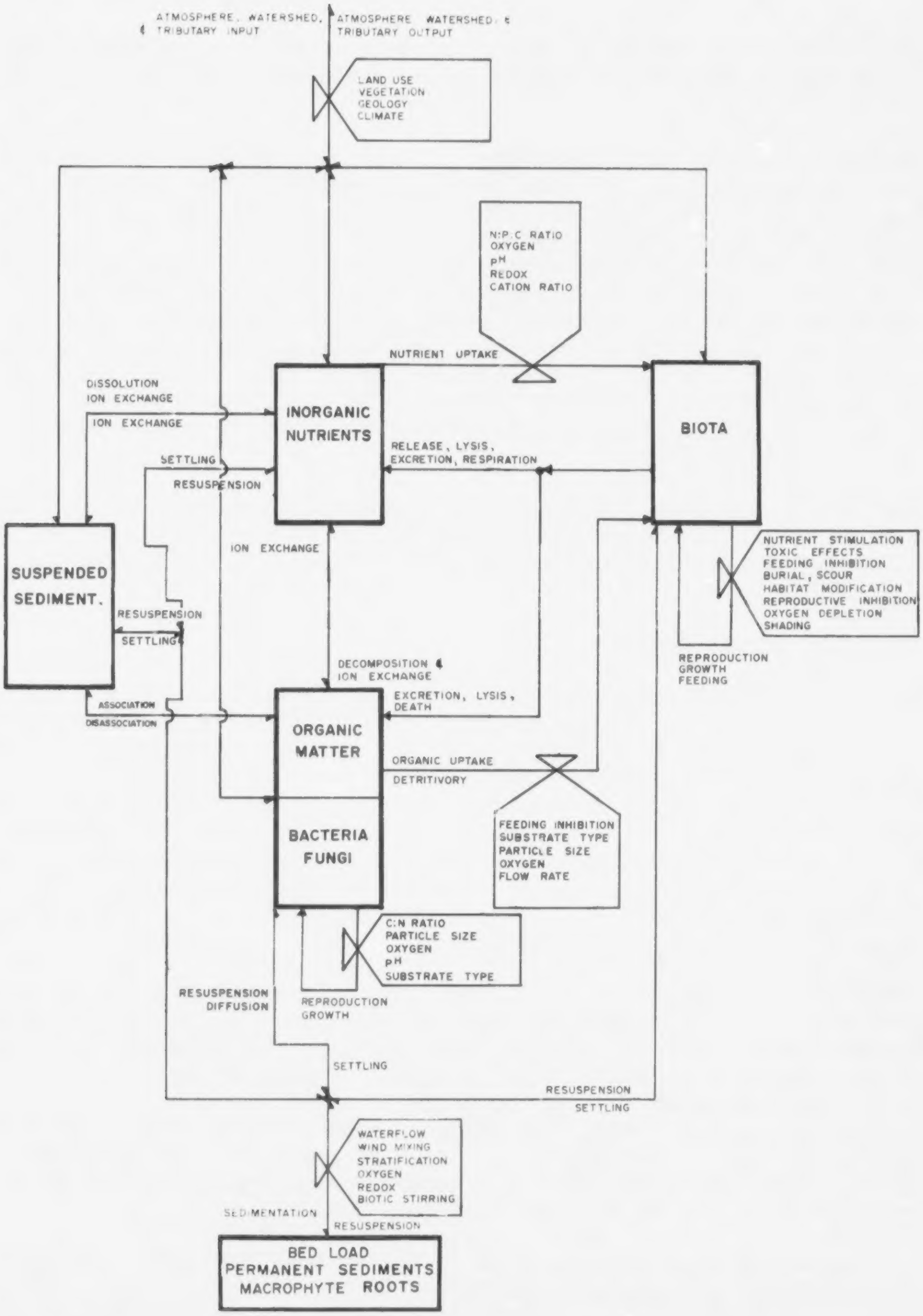
ATMOSPHERE, WATERSHED, & TRIBUTARY INPUT
ATMOSPHERE WATERSHED, & TRIBUTARY OUTPUT
LAND USE
VEGETATION
GEOLOGY
CLIMATE
N:P:C RATIO
OXYGEN
pH
REDOX
CATION RATIO
NUTRIENT UPTAKE
DISSOLUTION
ION EXCHANGE
ION EXCHANGE
INORGANIC NUTRIENTS
BIOTA
RELEASE, LYSIS, EXCRETION, RESPIRATION
SETTLING
RESUSPENSION
ION EXCHANGE
SUSPENDED SEDIMENT.
RESUSPENSION
SETTLING
NUTRIENT STIMULATION
TOXIC EFFECTS
FEEDING INHIBITION
BURIAL, SCOUR
HABITAT MODIFICATION
REPRODUCTIVE INHIBITION
OXYGEN DEPLETION
SHADING
REPRODUCTION
GROWTH
FEEDING
DECOMPOSITION & ION EXCHANGE
EXCRETION, LYSIS, DEATH
ASSOCIATION
DISASSOCIATION
ORGANIC MATTER
ORGANIC UPTAKE
DETRITIVORY
BACTERIA FUNGI
FEEDING INHIBITION
SUBSTRATE TYPE
PARTICLE SIZE
OXYGEN
FLOW RATE
C:N RATIO
PARTICLE SIZE
OXYGEN
pH
SUBSTRATE TYPE
RESUSPENSION DIFFUSION
REPRODUCTION GROWTH
SETTLING
RESUSPENSION
SETTLING
WATERFLOW
WIND MIXING
STRATIFICATION
OXYGEN
REDOX
BIOTIC STIRRING
SEDIMENTATION
RESUSPENSION
BED LOAD
PERMANENT SEDIMENTS
MACROPHYTE ROOTS

Fig. 10.6. Sediment-nutrient interactions at a coarse level of resolution. Major biota, nutrient, and sediment pools are shown in compartments. Lines indicate material flows, with the controls on these flows also indicated. Single headed arrows are used when the opposite directions of flow are labelled.

lack significant clay levels, or when available exchange sites are filled, little sorbing occurs and the ammonia formed diffuses upward (Brezonik and Fox 1976).

Sediments contain large quantities of nutrients which are potentially an internal nutrient source. All lake sediments contain higher nutrient concentrations than the overlying water. The concentration of inorganic or organic nutrients in the water column gives little indication of the amount present in sediments and the two pools may differ by several orders or magnitude (Wetzel 1975). A mean value of total phosphorus in the sediments of 16 Wisconsin lakes was 2550 mg/kg dry weight (Armstrong et al. 1971), although the range varied from 730 to 7000 mg/kg dry weight. Lake sediments generally have from 50 to 200 kg N/ha in the upper 10 cm of sediment (Keeney 1976). The upper 4 cm of sediment may serve as the immediate source of ammonia to overlying waters, but as much as 16 cm of sediment may contribute ammonia to the water column (Byrnes et al. 1972).

Release of nutrients from sediments is not only a function of nutrient concentration, but also is dependent upon such environmental factors as redox conditions and the presence of oxygen, various ions, pH, physical mixing, and organic matter.

Redox and Oxygen Levels:

The oxidation-reduction status of sediments influences not only the release but also the transformations of nutrients. Redox potential is usually reported in terms of pE or Eh (millivolts, mV). At the sediment-water interface Eh will range from +100 to +350 mV in the presence of oxygen (Turner and Patrick 1968; Keeney 1973). Sediments may remain in a reduced condition even if oxygen is present in the water column (Graetz et al. 1973). Sediments become more reduced as the hypolimnion becomes anoxic, with Eh values ranging from 0 to -250 mV (Keeney 1973). When oxygen becomes unavailable, alternate electron acceptors are used. Nitrate is the first alternative electron acceptor resulting in release of reduced nitrogen forms.

Whether or not anaerobic conditions in the hypolimnion result in a greater nutrient release from sediments is currently debated. Following the studies of Mortimer (1941, 1942), it generally was accepted that reducing conditions in the sediments and in the hypolimnion caused release of adsorbed phosphorus compounds from complexes. As long as an oxidized microzone at the sediment-water interface is maintained, most of the phosphorus will be retained and unavailable to biota. When oxygen depletion increases and the redox potential is decreased, previously adsorbed phosphorus becomes free to move from the sediments (Li et al. 1972; Lean and Charlton 1976).

In one recent study phosphorus was released from sediments under anaerobic conditions but not under aerobic conditions (Fillos and Biswas 1976). However, other studies contradict these observations indicating that phosphorus compounds bound in sediments are not affected significantly by the presence or absence of oxygen (Schindler et al. 1977). In another study phosphorus release was slower under aerobic conditions than under anaerobic conditions but rapid enough to play a role in the internal cycling of phosphorus (Lee et al. 1977).

Many studies also describe increased nitrogen release under anaerobic conditions (Mortimer 1941; Graetz et al. 1973). However, in some lakes, the release may not be different under different oxygen regimes or release may even be greater under aerobic conditions (Austin and Lee 1973; Brezonik and Fox 1976). Sediment bound ammonia is not a large source of nitrogen to the water. Instead, most sediment nitrogen is organic and major exchanges are biologically mediated. Under aerobic conditions, increased microbial assimilation and increased nitrification might result in less ammonium release upward. Observations of increased ammonium release, when the hypolimnion oxygen levels are low, also may be a result of increased upward diffusion when high productivity depletes nutrients in the water.

The causes of nutrient release from sediments and its usefulness to biota are not yet understood. Aquatic systems undergoing decreases in water column oxygen are more likely to be productive systems with higher nutrient levels in the sediments available for release upward. Therefore, nutrient release may not be a function of aerobic versus anaerobic conditions, but might result from increased decomposition rates. In addition, nutrients released from sediments under anaerobic conditions may not be available to biota since the thermocline may represent an impermeable barrier. To date most experiments on this subject have been performed in the lab and may not simulate actual conditions well. In situ experiments in a variety of aquatic systems are needed to determine the influence of oxygen on release of nutrients.

Ions:

An exchange of nutrients between the sediments and the overlying water will depend on the forms and charges of various ions present. The organic and inorganic sediment fractions often are very reactive. Humic substances may form complexes with di- and tri-valent cations, bind anions in ion exchange reactions (e.g., PO_4), and often are adsorbed strongly by clay surfaces. Clays may exchange cations (Grim 1968; Malcom and Kennedy 1970), provide sites for scavenging microbes, and may adsorb iron and manganese oxides. Iron and manganese oxides also enter into cation and anion exchange reactions (Jenne 1968; Malcolm and Kennedy 1970; Greenland 1971; Schnitzer and Kahn 1972; Paerl 1977). Several factors controlling these reactions include: pH, pE, (or Eh), ionic strength, cation exchange capacity, the type and form of ion being exchanged or absorbed, and the particle size and composition of the reacting surface.

Inorganic phosphate occurs in forms of salts of orthophosphate consisting of fluoro, oxy-, and hydroxy-phosphates of mainly Fe, Al, Ca, Mg, and Mn (Levesque and Schnitzer 1967). Gessner (1939) showed that phosphate was removed from solution after addition of calcium carbonate due to carbonate-phosphate co-precipitation. A linear relationship was found between calcium carbonate addition and phosphorus depletion in highly alkaline waters. The precipitation of calcium phosphate as apatite is increased under high $CaCO_3$ levels (Emerson 1976). Although apatite is one of the least soluble phosphate minerals in freshwater, partial dissociation of orthophosphate from apatite crystals (enough to support some cultures of algae) has been observed (Smith et al. 1978). Iron can complex with phosphorus under aerobic conditions. When conditions become anoxic, phosphate-ferric iron is reduced to a phosphate-ferrous iron complex which is more soluble, and phosphorus unbinds from the complex releasing phosphorus to the hypolimnion (Stumm and Morgan 1970). Iron also may compete with ammonium for sites on clay complexes causing the release of ammonium in iron-rich environments (Keeney 1976).

pH:

Due to the overriding influence of the redox system, most aquatic systems show little seasonal pH shifts (Stumm and Morgan, 1970). However, pH shifts have been noted in eutrophic lakes. For example, at spring overturn the hypolimnetic waters of Lake Mendota are about pH 8, while during summer stratification the pH is near 6.5 (Keeney 1976). Softwater systems may show a greater fluctuation in pH over time due to the absence of a $CaCO_2$ buffering system.

The role of pH in sediments in relation to phosphorus release is not clear. The orthophosphate content of sediments does not appear to be affected by pH in the neutral to slightly alkaline range (Kamp-Nielsen 1975; Lee et al. 1977). However, the pH of the sediment, when acidic, may stimulate phosphorus release to the water (MacPherson et al. 1958).

During stratification, increases in the hydronium ion, which is an effective competitor for exchange sites occupied by NH_4, may result in a greater release of ammonium to the water.

Recently, investigations have been initiated which examine the influence on water bodies of increased acidity in rainfall associated with cultural activities. Natural buffering systems may be exceeded, particularly in softwater systems. As pH values decline below 6, detrimental effects on organisms will be observed (Schindler 1979) and nutrient transformations may be altered. Microbial nitrogen transformations occur at a more rapid rate in calcareous sediments of hardwater lakes than in noncalcareous sediments from softwater lakes. Additions of $CaCO_3$ to noncalcareous sediments increased rates of ammonification, nitrification, and nitrogen fixation (Chen and Keeney 1973). Lower amounts of ammonia were found in the interstitial water in acid sediments of a softwater lake (Keeney et al. 1970).

Mixing:

Mixing has been considered to be an important factor influencing nutrient release from sediments. Most experiments demonstrating the importance of mixing, however, have been performed in the lab. In situ levels of turbulence as a result of wind action, underwater currents, gas bubbling, and stirring by benthic organisms can only be estimated (Brezonik 1973; Petr 1977; Ryding and Forsberg 1977). The degree of mixing also will depend on the sharpness of the mud-water interface, the type of sediment, and water depth (Lee 1970). In shallow lakes, mixing of sediments by wind or wave action or by turnover can be significant in nutrient release to the water (Zicher et al. 1956).

Seasonal overturn may result in the release of some nutrients but not others from the sediments to the water column. The nitrogen to phosphorus ratio of nutrients released from the sediments in Lake Kinnert, Israel, was 71 to 1 (Serruya 1974). The sediments were acting as a source of nitrogen as a sink for phosphorus in this phosphorus limited lake.

Lab studies show that turbulence increases nutrient release at least initially by release of interstitial pore water through suspension of sediment particles (Brezonik and Fox 1976). Continued mixing might prevent a large buildup of nutrients in pore water. Diffusion is a slow process which may normally have little importance compared to mixing in releasing nutrients to the water column, but diffusion may become a significant process during the static condition encountered during stratification (Gahler 1969; Runnells 1969; Stumm and Leckie 1971).

Organic Matter:

Organic matter can play an important role in the initial binding of phosphorus (Harter 1969). Phosphate is adsorbed through an anion exchange reaction, with phosphate ions replacing hydroxyl ions in the organic matter. Until the adsorbed phosphorus is precipitated by iron or aluminum the sediments may be capable of releasing phosphorus from the anion exchange sites to the overlying water. In a eutrophic condition, where sediments are normally high in organic matter, phosphorus adsorbed to organic matter could influence the nutrient status in the water. Organic matter can interfere with phosphorus precipitation as $Ca_3(PO_4)_2$ by complexing with calcium and thus releasing the phosphate (Levesque and Schnitzer 1967).

The level of organic matter present in sediments should influence quantities of inorganic nutrients released since decomposition of the organic matter is the source of many of these nutrients. A distinct, short-term increase in inorganic nitrogen released from lake sediments after detrital additions was found in lab experiments (Brezonik and Fox 1976). It was hypothesized that nutrients released from sediments arise from recently deposited detritus rather than from older sediments. Presumably, recently deposited detritus will have less time to become bound to sediments, will have proportionally more biologically degradable substances, and will be physically closer to the water-sediment interface where exchanges occur.

Biological Control of Nutrient Flux

Primary Producers - Algae:

Primary producers have been shown to upset the nutrient equilibrium between sediments and water. Following the algal uptake of nutrients from the water column, the system tends toward equilibrium by releasing nutrients from the mud. The main source of phosphate for the production of phytoplankton in an unfertilized pond was released from sediments (Hepher 1966). A tenfold increase in the growth rate of *Scenedesmus obliquus* was observed when it adsorbed phosphorus released from lake muds (Golterman et al. 1969).

Primary Producers - Macrophytes:

Macrophytes also play a role in the exchange of nutrients between sediments and water by acting as nutrient pumps and releasing nutrients from the sediments into the overlying water (McRoy and Barsdate 1970; McRoy et al. 1972;

McRoy and Goering 1974; Toetz 1974). Nutrients can be absorbed by either roots or foilage depending on the relative concentrations of nutrients in the water and sediments (Denny 1972). They may be translocated through the plant to the roots and sediments from the overlying water or be translocated to the leaves with some nutrient release into the water (Nichols and Keeney 1976; Twilley et al. 1977). While growing, macrophytes have the ability to give off oxygen and transmit nutrients to the water column. Upon death and decay they may sink to sediments, carrying nutrients downward and creating a large oxygen demand as they decay.

Bacteria:

Bacteria in anaerobic sediments contribute relatively little to the phosphorus flux from water to sediments. Under aerobic conditions the transport of phosphorus to the sediments by bacteria increases (Hayes 1955). Two mechanisms are postulated by which phosphorus can be maintained in the water column. First bacteria in the mud, upon decomposition, may accelerate release of phosphate back to the water, Second, bacteria in the water column may rapidly take up phosphate, preventing chemical absorption by mud. The bacteria may convert phosphate into organic compounds by incorporating it into their cells making it available at a later time. If bacterial numbers are high, then the role of bacteria in phosphorus cycling in the overlying water may be significant (Hayes and Phillips 1958).

Bacteria play a major role in nitrogen exchanges between the sediment and water column. Most microbial transformations of nitrogen occur in the sediments or are influenced by sediment conditions, especially ammonification, nitrification, and denitrification. Microbial components of sediments are important not only in directly mediating transformations of nutrients, but also indirectly in their ability to alter pH and oxygen concentrations, and to produce gas (Brezonik 1973).

Higher Organisms:

The major roles of benthic organisms in nutrient exchanges at the sediment-water interface are mixing and aeration of sediments and detritivory. The effectiveness of the sediments in retaining phosphorus under aerobic conditions may be a result of mixing of sediments several centimeters deep by benthic organisms which causes an increase in the oxidized microzone (Davis et al. 1975; Schindler 1975). On the other hand, chironomid movement has been shown to increase phosphate release to the water (Gallepp 1976). Mixing by bottom feeding fish and aquatic insects also may occur. In addition, insect emergence from the sediment may result in a loss of nutrients from the system (Vallentyne 1952; Neame 1977). The role of insects in nutrient removal may depend upon the concentration and forms of sediment nutrients, numbers of insects, or the present trophic state of the water. Detritivores assimilate organic matter thereby making nutrients available by passage through the feeding webs.

10.2.3 Evidence of Nutrient Impact on Biota

In this section evidence of biotic response to external nutrient loading is examined. Studies of this type are important in understanding how cultural activities may influence water quality. Presently, most of these impact studies concentrate on responses of primary producers in lakes, although an attempt was made to include impact studies in other system types and on higher trophic levels.

Since impact studies rely on the ability to detect increased productivity the methods used should be examined for their accuracy. Considerable spatial variation in productivity is seen in large lakes (Sorokin 1959; Goldman 1960; Goldman 1961), requiring sampling at several stations. There also may be daily or seasonal fluctuations in limiting nutrients so that responses will depend on the time of nutrient enrichment. In addition, transient and steady state responses to nutrient additions may be different (Goldman and Carter 1965). Lab studies should be carefully scrutinized since results may have only limited applicability to processes actually occurring in situ. Containers placed in the water may exclude important exchanges between surrounding water and the sediments. Whole system studies, although time consuming and expensive, may provide important information that might be lost in smaller scale experiments.

Impact of Nutrients in Streams

Nutrient concentrations in streams are closely related to land use practices (Omernik 1976, 1977). However, within a stream nutrient concentrations and nutrients removed from the watershed vary over time with changes in flow patterns. Particularly for small watersheds, greatest phosphorus export may be associated with infrequent periods of high flow (Allum et al. 1977). Therefore, the impact of nutrients in streams will not only depend upon watershed activities but also will vary with different flow regimes within one stream.

Nutrients may not increase primary productivity in streams since stream behavior may be more influenced by overriding physical factors than by nutrient concentrations. Williams (1964) reported that physical factors may determine phytoplankton presence regardless of nutrient availability. Stream characteristics that may influence primary productivity include current speed, slope, depth, and the stream order.

A stream system in Iowa with high initial phosphate and nitrate levels did not respond to nitrogen and phosphorus input (Kilkus et al. 1975). Inorganic phosphorus and nitrogen levels were high and algal populations were regulated by flow, drainage area, and temperature. During low flow periods, high chlorophyll values were found. It was concluded that neither phosphorus nor nitrogen were limiting.

In streams diurnal fluctuations of oxygen correlated well with estimated nutrient loadings and trophic conditions in three rivers in Michigan (the Jordan with a relatively low nutrient content; the more enriched Au Sable; and the highly enriched Red Cedar) (Ball et al. 1973). Higher diurnal oxygen variations occurred in the more enriched river systems. Phosphorus tissue content of macrophytes was related to the concentration of nutrients in the water, but the standing crop of plants was controlled by stream morphology (configuration, flow, and turbidity) rather than levels of nutrient loading.

In autotrophic reaches of low nutrient streams addition of nutrients may have a stimulatory effect. Benthic algal biomass increased in Carnation Creek, Vancouver Island, when phosphorus was added with or without added nitrogen. Nitrate addition alone had little effect on algal growth (Stockner and Shortreed 1978).

Frequently, nutrient additions result in enhanced productivity due to an interaction of nutrients. When nutrient interactions occur, the system responds most to two or more nutrients added together rather than to additions of a single nutrient. The N:P ratio can shift frequently and intermediate values between phosphorus limitation and nitrogen limitation are encountered for many species. Several species in the natural assemblage may respond to added nitrogen while others respond to added phosphorus. Nitrogen and phosphorus interacted to influence biotic response in streams in the Midlands of Great Britain. In situ experiments in various river waters showed that the highest nitrogen level increased growth at the lowest phosphorus level. A positive correlation between the mean annual dry weight of *Cladophora* and the mean annual phosphorus concentration was seen. No significant correlation between nitrogen and dry weight was observed (Pitcairn and Hawkes 1973).

Impact of Nutrients in Reservoirs

A few examples of rapid eutrophication in reservoirs are documented, including impoundments in Arkansas (Geerhart 1969), North Dakota (Peterka 1970), Illinois (Wang and Evans 1970), and Oklahoma (Toetz 1972). Since nutrient loading levels generally are high, reservoirs may not respond to nutrient additions. Orthophosphate, total phosphate, nitrate, and ammonia levels were not correlated with chlorophyll *a* concentrations in eastern Nebraska reservoirs undergoing eutrophication. These nutrients may not be limiting because of rapid recycling. Physical factors such as temperature, turbidity, and day of the year appeared to correlate most highly with chlorophyll *a* concentrations (Schwartzkopf and Hergenrader 1978).

On the other hand, some reservoirs receive nutrient loading equivalent to that which should produce a eutrophic system, but due to high flushing or sedimentation rates they remain oligomesotrophic (Bachman and Canfield 1979; Lind 1979).

Impacts of Nutrients in Lakes

Based upon the literature reviewed, the major influence of nutrients is a stimulation of primary productivity in lakes. The degree of impact of nutrient addition has been related to initial nutrient concentrations. Therefore, the evidence for impacts is divided into sections based on trophic status.

Oligotrophic Waters:

Oligotrophic waters generally show high sensitivity to nutrient loading. Since they have low nutrient concentrations, factors limiting productivity may change frequently with minor changes in loading or physical conditions. Most nutrients have a short residence time in the water column, and they are flushed from the system or are lost to sediments. Sediments may not contribute greatly to epilimnetic nutrients, because of extreme depth, because the oxidized hypolimnion acts as a barrier, or because of little decomposition. Diatoms are among the dominant phytoplankton at low nutrient concentrations. At death, diatoms sink rapidly, removing nutrients from the epilimnion. The only significant recycling of nutrients is from plant lysis and excretion by consumers. Consumer numbers will be low, so this source of nutrients will be minimal.

Many oligotrophic systems appear to be phosphorus limited. Data have been compiled relating trophic state to phosphorus loading for 15 oligotrophic lakes. Phosphorus limitation for these lakes, located mainly in the continental United States, was found through the use of algal assays and interpretation of N:P concentration ratios (Yeasted and Morel 1978). Actual phosphorus loading to an oligotrophic lake in the Experimental Lakes Area (Lake 227) revealed that phosphorus caused a positive growth response in phytoplankton. The addition of nitrogen, alone, did not result in any increase in algal standing crop (Schindler et al. 1973).

Nitrogen may be the primary limiting nutrient in other oligotrophic waters. Phytoplankton growth, as measured by ^{14}C uptake, was stimulated in all treatments in which nitrate was added to Lake Tahoe, California (Goldman and Carter 1965; Goldman and Armstrong 1969). Phosphorus additions did not stimulate growth even when added with nitrogen.

Nutrients frequently interact in stimulating productivity in oligotrophic lakes. For example, phytoplankton in Mirror Lake, New Hampshire, was stimulated by additions of nitrogen and phosphorus together (Gerhart 1975).

An increase in photosynthesis and in phytoplankton biomass was found when nitrogen and phosphorus were added to experimental ponds (McIntire and Bond 1962). Diatoms were the dominant phytoplankton in the absence of enrichment. Codominance of diatoms and desmids resulted in nitrate enriched ponds. With nitrate and phosphorus enrichment, flagellates were most important. Zooplankton densities followed fluctuations in phytoplankton abundance. Crustaceans and rotifers, especially, became abundant in enriched ponds. Following a dense algal bloom and death in a highly enriched pond, organic food was available for larval midges (Tendipedidae), a few horsehair worms (Gordius), and dragonfly naiads (Libellulidae). This pond supported the highest benthic biomass with the total dry weight of two samples being about 15 times that of an unenriched pond.

Individual additions of nutrients to oligotrophic Eagle Lake, California, produced little, if any, response; therefore, all essential nutrients except one were added in each culture (Maslin and Boles 1978). The shallow north basin was limited most severely by iron and phosphorus, which were tied up in oxidized sediments. The anoxic conditions in the south basin resulted in a regeneration of these nutrients so that nitrogen was more limiting. Chlorophyll increased in both basins in the presence of added nitrogen, phosphorus, iron, and sulfur. Nitrogen and phosphorus were most limiting; sulfur and iron were also limiting, but the order of importance was opposite in the two basins. When one of these elements was removed, total growth of phytoplankton was reduced to less than 30 percent. This study also demonstrated the importance of physical characteristics such as mean depth and flow rate in determining the most limiting nutrient. It showed variations in response in a lake with watersheds exhibiting differences in climate, topography, and volume.

Nitrogen, phosphorus, and NTA (a chelator) were added to algal communities from Lake 240 (Experimental Lake Area, Ontario) and from Katherine Lake, Manitoba (Stockner and Evans 1974). Phosphorus stimulated growth more than nitrogen and nitrogen more than NTA in Lake 240. The addition of NTA generally did not function in a catalytic capacity as might be expected. Lake 240 had an initial N:P ratio of 18:1 as measured by cellular contents of periphyton, and might be expected to respond mainly to phosphorus. However, an interaction was observed whereby median concentrations of both nitrogen and phosphorus yielded greatest growth. Lake Katherine had an N:P ratio of 9:1 initially and might be expected to show a greater response to nitrogen additions although added nutrients of any kind generally inhibited growth in Lake Katherine. The species present were most likely species that have optimal growth at low nutrient concentrations, and neither nutrient may have been limiting at an N:P of 9:1.

Other compounds including silica (Schelske et al. 1972, 1975), dissolved organic matter (Wetzel 1966a), EDTA, NTA, and other chelators (Stoermer et al. 1978) may interact with nitrogen or phosphorus and play a significant role in regulating productivity. In oligotrophic lakes all over the world (Africa, Alaska, California, New Zealand, and Anarctica), 23 of the 28 lakes observed were deficient in at least one trace element (Goldman 1971). Combinations of nutrients and trace elements were often necessary to stimulate production. Several lakes were deficient in molybdenum, which was needed by nitrogen fixers.

Nutrients added alone to the hardwater marl lakes of Indiana had little effect and became rapidly unavailable (Wetzel 1966b). These lakes are characterized by low productivity, high pH, and an excess of divalent cations and carbonates. However with the addition of organic matter and nutrients, stimulation of phytoplankton was observed. These organic compounds act as chelators, increasing the availability of nutrients. A significant stimulation of phytoplankton also was seen in less productive Crooked Lake with the addition of organic chelators. In the more productive Little Crooked Lake no stimulation of phytoplankton was observed.

A large increase in phytoplankton productivity (492 percent) resulted from addition of nitrogen, phosphorus, and EDTA in Lake Crystal, Michigan (Jordan and Bender 1973). Seven of 15 species examined responded to nutrient additions. Species composition also changed with enrichment.

Oligotrophic systems, especially, may shift from one limiting nutrient to another seasonally, since all nutrient levels are low and the ratios may change frequently. In three oligotrophic Alaskan lakes, a nitrogen deficiency occurred only during the summer as measured by nitrate stimulation of ^{14}C uptake by lake phytoplankton in situ, and in experimental cultures (Goldman 1960).

Mesotrophic Waters:

In mesotrophic lakes, anoxic conditions may be encountered seasonally. Mesotrophic systems may be unstable since additional nutrient contributions from external sources and from internal cycling can act to stimulate productivity and rapidly accelerate the process of eutrophication. On the other hand, some systems may be maintained at an intermediate level of productivity. For example, softwater systems generally are low in productivity and may not respond as quickly to loading since bacterial activity may be slower at low pH (Chen et al. 1972a, 1972b; Byrnes et al. 1972). The cold conditions of arctic lakes can result in less year round bacterial activity and slow down eutrophication. High flushing rates also will dilute nutrient concentrations, decreasing productivity. However, many temperate mesotrophic systems will tend to become eutrophic as a result of internal nutrient sources, even if surface nutrient loading is diminished.

Mesotrophic lakes generally are more limited by phosphorus than nitrogen. As phytoplankton species change and numbers increase, more nutrients are released into the system through cell lysing. Zooplankton numbers may accumulate in response to increased numbers of phytoplankton and add to the regeneration of epilimnetic nutrients by excretion. High phosphorus levels allow nitrogen fixing blue-green algae to become established. Blue-greens may become dominant by secretion of substances which inhibit diatoms (Keating 1978). Nitrogen fixation may add substantially to the nitrogen loading, preventing nitrogen limitation in the system. Higher organic carbon levels associated with the increased productivity also stimulate bacterial nitrogen fixation.

In Lake Washington, an increase in phosphorus favored production of blue-greens, with green algae being less favored and diatoms least abundant (Welch et al. 1975). Since receiving sewage, Lake Washington showed symptoms of eutrophication, e.g., increased nutrient concentrations; increased phytoplankton and zooplankton biomass, increased chlorophyll _a_ concentrations in the epilimnion, decreased transparency, decreased oxygen concentrations in the hypolimnion, and a shift from diatom and dinoflagellate dominance to blue-green dominance (Edmondson et al. 1956; Edmondson 1961). Diversion of the sewage resulted in a decrease in concentrations of phosphorus by 72 percent and in concentrations of nitrogen by 20 percent (Edmondson 1966, 1969, 1970).

Two neighboring arctic lakes, oligotrophic Char and mesotrophic Meretta Lake, were compared by Schindler et al. (1974). Standing crops of phytoplankton were 10-100 times higher in Meretta Lake than in Char Lake, and differences in species composition were noted. Phosphorus addition was required to initiate a growth response in Char Lake, although additions of both nitrogen and phosphorus resulted in the largest responses, indicating nutrient interaction. The dominant phytoplankton changed to Peridineae, the same group dominating Lake Meretta. _Limnocalanus macrurus_ disappeared from Meretta Lake and has not been replaced by another zooplankter. The Arctic Char (_Salvelinus alpinus_) also might be having difficulties surviving in Lake Meretta. The eggs or fry which over-winter on the bottom are dying as a result of altered oxygen, food, or sediment conditions.

The upper Great Lakes vary in trophic state from oligotrophic to eutrophic, and trophic conditions also vary within the lakes. Near cities or nutrient-rich rivers, conditions may be eutrophic while the interior of the lake may be oligotrophic. Differences in species and abundance of diatoms as well as differences in nutrient and pigment concentrations are observed when comparing inshore and offshore waters of Lake Michigan (Holland and Beeton 1972). Greater numbers of diatoms are seen inshore in waters that are nutrient rich.

Phosphorus additions have been shown to increase chlorophyll concentration and the rate of carbon fixation in phytoplankton in Lake Michigan (Schelske et al. 1975). Also, in Lake Michigan, phytoplankton response varied for species within the same division. In the Bacillariophyta, growth rates of *Nitzschia* and *Fragilaria* increased with addition of nitrate at low and high levels of phosphorus. In *Stephanodiscus* and *Navicula*, high nitrate levels caused inhibition of growth, which was magnified at high phosphorus levels (Stoermer et al. 1978).

Nitrate concentrations generally are high in the upper Great Lakes which appear to be limited by phosphorus (Schelske and Roth 1973; Schelske et al. 1974). Although nutrient enrichment experiments indicated highest chlorophyll *a* production with phosphorus enrichment, some indications of phosphorus and nitrogen interactions were observed (Schelske et al. 1974). Nitrogen enrichment in Lake Michigan had an effect at the species level even though no effect on total ^{14}C uptake was observed (Stoermer et al. 1978). A shift from blue-green to diatom dominance occurred.

Crustacean zooplankton in the Great Lakes were examined with regard to the trophic status of each lake (Patalas 1972; Watson 1974). A decreased significance of calanoids and an increased predominance of cyclopoids and cladocerans were seen as a general trend from oligotrophic Lake Superior to eutrophic Lake Erie. The average crustacean abundance was related to temperature, chlorophyll *a* concentrations, and phosphorus loading. Although Lake Erie had an increased biomass of zooplankton, larger organisms were observed in Lakes Superior and Huron. Increased numbers of oligochaetes in the benthos of the Great Lakes occurred under more eutrophic conditions (Cook and Johnson 1974). In addition, large populations of tubificid worms in highly polluted areas were seen.

Eutrophic Waters:

Shallow systems rapidly respond to increased nutrient loading by becoming eutrophic. Even large lakes can become eutrophic as they continue to receive nutrients. Once eutrophic, internal nutrient sources from sediments and biota may maintain eutrophic conditions in freshwater systems, even with the absence of significant external loading.

Many measurements of algal response indicate that phosphorus may be limiting in many enriched waters. In several lakes the chlorophyll *a* concentration was measured along with spring total phosphorus concentration (Sakamoto 1966; Dillon and Rigler 1974; Chapra and Tarapchak 1976). A significant correlation ($r = 0.93$) was determined for predicting the average summer chlorophyll *a* concentration based on spring total phosphorus. In four Iowa lakes a reduction in annual phosphorus input resulted in a smaller algal bloom (Jones and Bachman 1975). All lakes had N:P ratios ranging from 13:1 to 30:1, suggesting phosphorus limiting conditions.

Eutrophic waters are frequently nitrogen limited. Nitrogen fixation is a slow process (McCarty 1970) and may not contribute sufficient nitrogen. Losses of nitrogen through denitrification also may be significant. In addition, phosphorus loading may exceed nitrogen loading, especially near urban areas. Sediment also may contribute phosphorus, particularly with increased loading of organic substances which may act as chelators, increasing the availability of phosphorus (Jordan and Bender 1973).

Growth of Microcystis, collected from blooms in two eutrophic Wisconsin lakes, was nitrogen limited, as determined by known optimal growth requirements (Gerloff and Skoog 1957). Nitrate stimulation of phytoplankton also was seen in eutrophic Green Lake, Seattle, Washington. Stimulation was observed in blue-greens but not in green algae or diatoms (Welch et al. 1972).

Lakes receiving wastewater may become limited by nitrogen since the N:P ratios of wastewater are frequently low. Nitrogen limited algal growth in five locations receiving wastewaters along the northeastern U.S. coast (Goldman 1976). The N:P ratios in the wastewater-seawater mixtures were between 4 and 12. Enrichment with phosphorus had no effect on algal growth, but nitrogen additions stimulated growth. However, coastal waters are frequently limited by nitrogen when they do not receive wastes.

Nutrient addition may indirectly influence higher trophic levels under eutrophic conditions. Partial or complete anoxic conditions resulting from decomposition of heavy algal blooms led to subsequent summer fish kills in southwestern Manitoba (Barica 1975).

There are many examples of culturally eutrophied systems which show changes in productivity and shifts in phytoplankton, fish, zooplankton, and benthic species due to sewage addition (Hasler 1947; Paloumpis and Starrett 1960; O'Brien and Denoyelles 1976; Casterlin and Reynolds 1977). Sewage effluent added to a small lake (Grasmere) in the English Lake District resulted in a change from a mesotrophic lake to a eutrophic lake (Hall et al. 1978). The specific nutrient or nutrients influencing the system are not always identified. The addition of fertilizer containing nitrogen, phosphorus, and potassium to experimental eutrophic ponds resulted in increased phytoplankton productivity (O'Brien and Denoyelles 1976). A direct relationship emerged between fertilizer level and chlorophyll a measurements.

In the National Eutrophication Survey from 1972 to 1975 over 800 lakes impacted by sewage treatment plant outfalls were studied. The phytoplankton in several of these lakes were examined using indices such as Nygaard's Trophic State (Nygaard 1949) and Palmer's Organic Pollution (Palmer 1969), as well as diversity and abundance indices to determine relationships between algal characteristics and trophic status (Hilgert et al. 1977; F. A. Morris et al. 1977; M. K. Morris et al. 1977, 1978a, 1978b; Taylor 1977; Williams et al. 1977, 1978; Hern et al. 1978). Generally, Cyanophyta, Euglenophyta, centric diatoms, and some chlorococcales were associated with eutrophic conditions, in annual phosphorus input resulted in a smaller algal bloom (Jones and Bachman 1975). All lakes had N:P ratios ranging from 13:1 to 30:1, suggesting phosphorus limiting conditions.

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Nutrient-algal relationships varied with season in Lake Lillinonah, Connecticut (EPA 1975). Growth of Selenastrum was stimulated by nitrogen additions in July and phosphorus additions in August, while blue-green algal growth was stimulated by phosphorus additions throughout the season. When phosphorus addition was reduced, biomass of blue-green algae was reduced correspondingly.

Many interacting factors may be working together to influence a system's response to nutrient addition. Factors such as chelators or physical parameters such as basin morphometry may influence the role of the primary limiting element (Mackereth 1953; Hutchinson 1957; Vallentyne 1957; Bninska et al. 1976). To obtain the most accurate account of the response, long term, whole lake studies are critical. Lakes in the Experimental Lakes Area (ELA) were fertilized with additions of phosphorus, nitrogen, and carbon over a period of years in order to observe biotic response to increased eutrophication (Schindler and co-workers 1971, 1973, 1975, 1977). Experiments demonstrated that carbon and nitrogen deficiencies of algae were corrected for by diffusion of atmospheric carbon dioxide into the water or by nitrogen fixation by blue-green algae. Even if phosphorus input was high, phytoplankton growth over time became proportional to phosphorus concentration. Hypolimnetic microplankton and sediments were the most efficient in rapidly removing phosphorus from the water suggesting that nutrient diversion to the hypolimnion of the lake may have a minimal effect in increasing algal blooms. During the six years of fertilization, input-output data indicated that the majority of phosphorus and nitrogen added was accumulated in the sediments. Even when hypolimnetic waters became anoxic, no net return of phosphorus was observed from the sediments to the water. Further whole lake studies are essential to the understanding of the nutrient dynamics in freshwaters.

10.2.4 Regionalization of Impacts

The National Eutrophication Survey was an important step in gaining nationwide baseline information on nutrient conditions in streams, lakes, and reservoirs across the country. However, the information obtained has some weaknesses for management use.

Nationwide patterns of nitrogen and phosphorus concentrations in streams were presented and linked to watershed activities (Omernik 1976, 1977). The stream data were collected from watersheds having only nonpoint inputs. Information was not obtained for streams impacted by point sources and no correlations were made between productivity levels and nutrient concentrations. Information appears to be lacking on any influence the various concentrations have on biota.

The data collected on lakes and reservoirs was obtained only from particular system types. Selection of study sites was limited to large systems impacted by sewage treatment plant outfalls and with mean hydraulic retention times of at least 30 days (Allum et al. 1977). Correlations between trophic state and phytoplankton species diversity and abundance were obtained for several lakes, although regional comparisons were not made. Trophic state classifications have been compared to the predictive models based on phosphorus loading for 39 eastern, mostly eutrophic, lakes (Hern et al. 1978). Disagreements were found of 14, 18, and 25 percent, respectively, for the Dillon (1975), Larsen and Mercier (1976), and Vollenweider (1975) models (discussed in section 10.3.1). These models should be applied to western lakes and impoundments and to lakes of other sizes and trophic classifications to determine how well the models predict whole system response. The situations where the models do not predict well should be examined to find an alternative model, such as a nitrogen loading model for nitrogen limited systems, which might predict response better.

The data obtained for streams should be compared with that obtained for lakes and impoundments to investigate possible relationships. An integration of nutrient concentration data with impacts on biota, including higher trophic levels, also needs to be done. Then decisions can be made for management, selecting either one system nationwide or using regional criteria; choosing physical and chemical measurements or biotic indices; and managing for system properties or for particular species of interest.

The examination of the literature on the impact of nutrient additions on biota reveals that data exist only for a few regions of the country. Most of the information available comes from the Northeast, Midwest, and Northwest. Even within these regions sufficient data are available for only a few bodies of water.

Although the various trophic categories may be found in every region, some regional trends may exist. Identification of these trends may be valuable for management procedures. As a result of this literature review, generalizations may be made. Most of the oligotrophic systems studied were either large, deep lakes or were hardwater systems. They were located near the Great Lakes regions of the country or in California. As expected, a variety of situations were observed. Depending upon nutrient ratios, a single nutrient may be limiting or the addition of several nutrients together may be required for stimulation of growth.

Few studies on mesotrophic systems were reported, perhaps because the mesotrophic condition is less stable and therefore less frequently observed. The mesotrophic condition was generally observed in a narrow area within a larger water body such as in the Great Lakes. In these studies phosphorus was the major limiting nutrient.

Studies on eutrophic systems were found for several regions of the country. Some lakes were limited by phosphorus and others by nitrogen, with the nutrient limiting a particular system being a function of local factors. The reservoirs and streams studied in the Midwest did not respond to additions of either phosphorus or nitrogen. One study on Michigan streams (Ball et al. 1973) of each trophic category revealed that plant standing crop was regulated by stream morphology rather than by nutrient loading.

10.3 PREDICTIONS OF BIOTIC RESPONSE TO IMPACTS

10.3.1 Models

Nutrient models are an important tool in predicting behavior following nutrient addition. Several nutrient mass balance budgets for various lakes and streams have been calculated taking into account the retention coefficient, flushing rate, mean depth, and areal loading (Schindler et al. 1971; Patalas 1972; Imboden 1974; Dillon 1974, 1975; Dillon and Rigler 1975; Kirschner 1975; Larsen and Mercier 1975, 1976; Snodgrass and O'Melia 1975; Vollenweider 1975; Eisenreich et al. 1977). These models are useful in comparing aquatic responses over a large number of systems.

Permissible and dangerous loading levels were originally established on an areal basis as a function of mean depth after examination of 30 lakes in Europe and North America (Vollenweider 1968). Performing similar analyses in the United States, specific critical loading levels separating oligotrophic and eutrophic waters were set at 0.2 - 0.5 g total $P/m^2/yr$ and 5 - 10 g total $N/m^2/yr$ (Bartsch 1972). However, not only depth but geomorphological factors confound simple relationships between loading, concentration, and algal production (Vollenweider 1976). Therefore, the loading graph for phosphorus was modified by plotting loading (L) versus mean depth ($\bar{z}$) divided by hydraulic residence time (Tw), the mean residence time of water (Fig. 10.7) This function predicts the trophic state of the water based on loading rates in phosphorus limited lakes. The hydraulic residence time integrates a number of limnological processes and significantly correlates with trophic state, although the causal relationships are not readily identifiable. A graph of this type for nitrogen was not derived, since relationships between nitrogen loading and trophic state are less clearly defined (NAS 1978). Figure 10.8 plots nitrogen loading as a function of mean depth only. Prediction of the trophic state in nitrogen or nonphosphorus limited lakes may not be related to residence time, and a predictor of the response in these systems needs to be developed.

However, while these models adequately employ loading and geomorphomentrical conditions to determine the system response to nutrient loading, they ignore the internal biotic cycling occurring within the system. The importance of internal nutrient dynamics, especially in eutrophic lakes with heavy sediment nutrient loads, has been stressed (Shapiro et al. 1975). A model that incorporates biological dynamics and has been validated in several European lakes is MS. CLEANER (Park et al. 1978). Although this model is expensive to use and requires considerable data input, application of this model to a variety of North American lakes may increase the understanding of system response.

A model based on physical processes was developed for predicting nutrient losses from watersheds to streams for various types of watersheds (Nan-Hsiung Ho 1978). This model is useful for indicating how nutrient inputs vary but does not include measurements of biotic impact. A model of PO_4-P sinks and sources in a river in Japan has been developed which takes into account not only the usual physical factors such as diffusion and flow, but also includes biological factors such as the role algae play in taking up and releasing

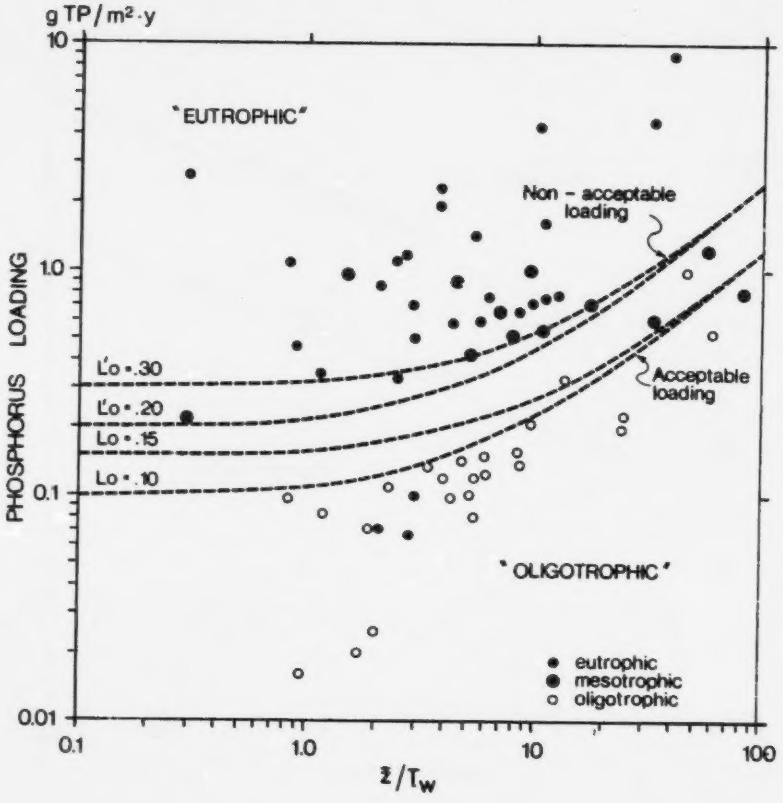

Fig. 10.7. Correlations of phosphorus loading levels with trophic status (From Vollenweider 1976.)

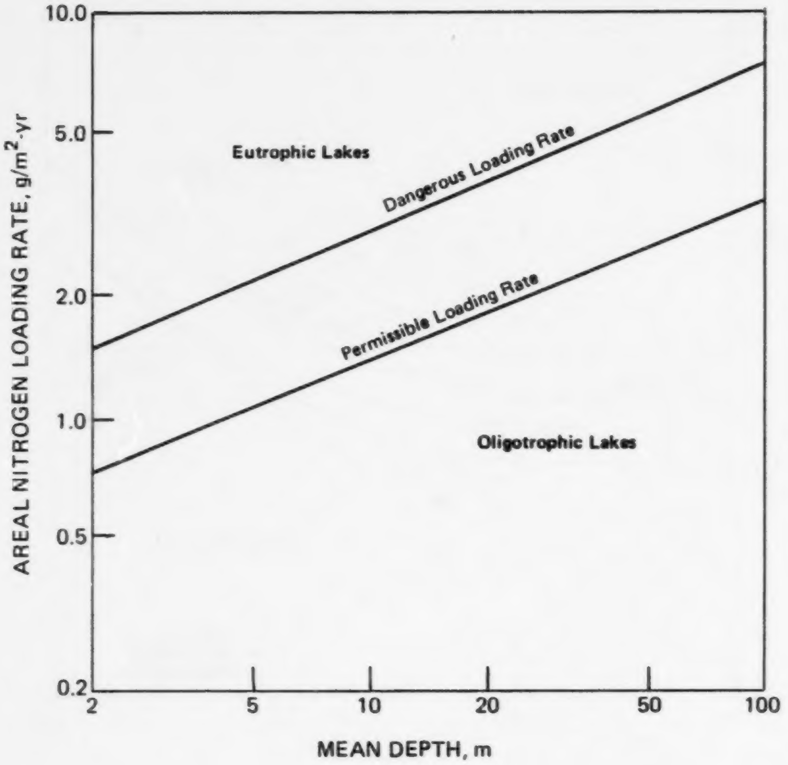

Fig. 10.8. Nitrogen loading related to trophic state. (From NAS 1978 based on Vollenweider 1968.)

PO_4-P in the river bed and in the flowing water (Aiba and Ohtake 1977). Stream modelling, however, has not received adequate consideration in relation to nutrients. This type of model is lacking due to problems in determining where and how much loading occurs (sources may be diffuse), problems in relating nutrient concentrations to impacts on biota, problems in sampling due to the "patchy" nature of streams, or because nutrients are not limiting in many streams.

For this report conceptual models have been developed indicating the major phosphorus and nitrogen flows through all trophic levels and including the controls on these flows (Fig. 10.9, 10.10). Figure 10.11 combines both nutrient flows at a coarse level to indicate the nutrient-biotic interactions that may occur in a system. Since the models are conceptual, they can be applied to various system types (lakes, streams, or reservoirs) by modification of flow rates and depth. However, a conceptual model of this type may have limited applications since it lacks quantification of flows and may be too cumbersome to use efficiently in predicting response for any type of system.

10.3.2 The Standard Aquatic Response

Although each aquatic system is unique, an attempt has been made to describe a standard response to nutrient addition based on the inputs, outputs, and the initial state of the system.

In an oligotrophic system the paths of most significant nutrient flows are indicated by number 1 in Figure 10.12. These flows are of relatively equal importance. As a system becomes more productive, flows indicated by number 1 increase, and those flows represented by number 2 may become more important. As long as loading is not excessive, an oligotrophic system is maintained. Most nutrients will be lost to sediments and little upward movement of nutrients occurs. Biotic recycling in the epilimnion is important in maintaining nutrients in the water column. With continued nutrient inputs, productivity increases, and the species composition of phytoplankton changes (diatoms to greens). If productivity is high, anoxic conditions may be encountered seasonally, indicative of a mesotrophic system. Many mesotrophic systems may tend to become eutrophic rapidly, even if surface nutrient loading is not high, due to the positive feedback from biotic cycling and from sediments. With high epilimnetic nutrient concentrations and high levels of productivity, nitrogen availability may decrease relative to phosphorus. Nitrogen fixation may then become important as a supplemental source of nitrogen. Once eutrophic, systems may be characterized by particularly high rates of some nutrient transformations, such as denitrification, which contributes to nitrogen limitation. Mesotrophic systems may rapidly become eutrophic as anoxic conditions prevail and as flows 1 and 2 increase.

Changes in primary productivity have profound influences on higher biota. As primary production rises, a shift in the dominant phytoplankton species may be seen (greens to blue-greens). A species shift to blue-greens will usually produce an undesirable food source for zooplankton, subsequently causing a decline in these organisms. Bottom fauna may be replaced by tubificid worms. In shallow systems where littoral areas are significant,

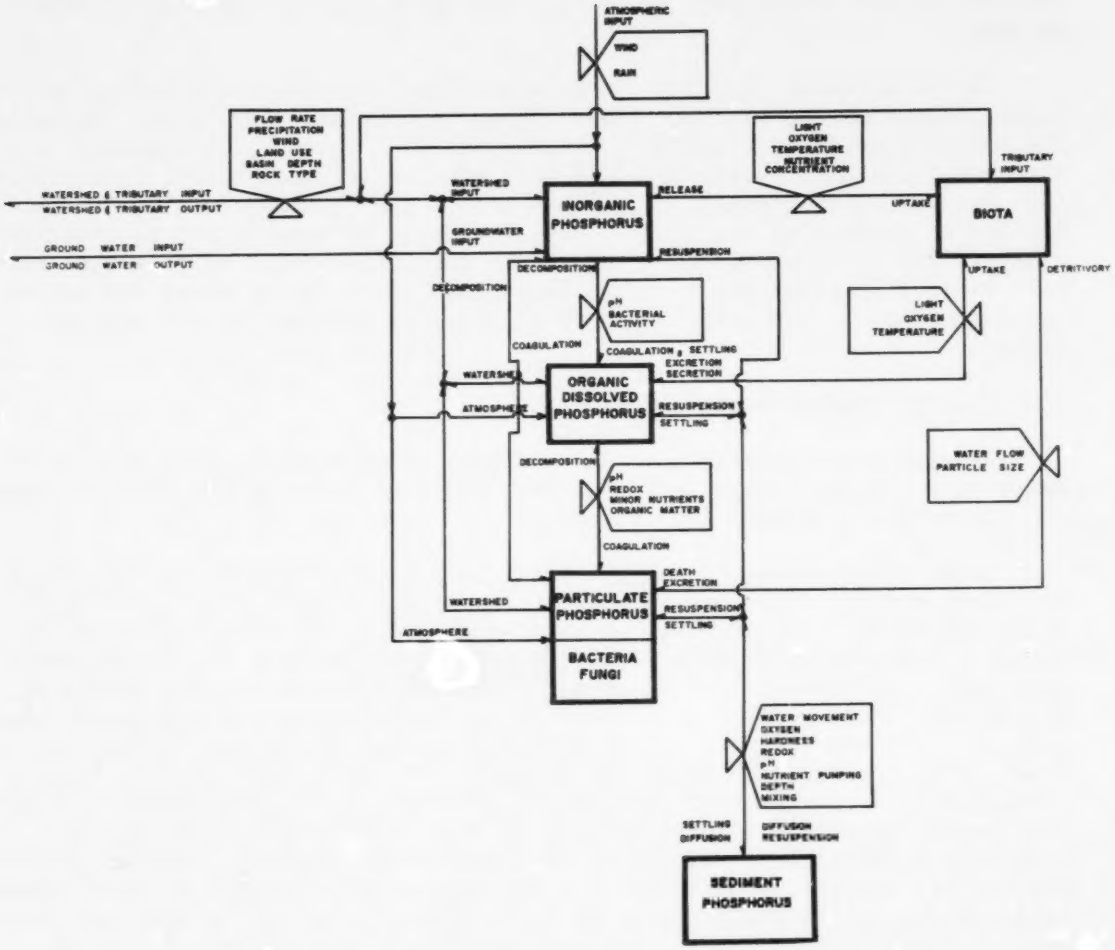
ATMOSPHERIC INPUT
WIND
RAIN
FLOW RATE
PRECIPITATION
WIND
LAND USE
BASIN DEPTH
ROCK TYPE
WATERSHED & TRIBUTARY INPUT
WATERSHED & TRIBUTARY OUTPUT
GROUND WATER INPUT
GROUND WATER OUTPUT
WATERSHED INPUT
GROUNDWATER INPUT
INORGANIC PHOSPHORUS
RELEASE
LIGHT
OXYGEN
TEMPERATURE
NUTRIENT CONCENTRATION
UPTAKE
TRIBUTARY INPUT
BIOTA
RESUSPENSION
DECOMPOSITION
DECOMPOSITION
pH
BACTERIAL ACTIVITY
UPTAKE
DETRITIVORY
LIGHT
OXYGEN
TEMPERATURE
COAGULATION
COAGULATION & SETTLING
EXCRETION
SECRETION
WATERSHED
ATMOSPHERE
ORGANIC DISSOLVED PHOSPHORUS
RESUSPENSION
SETTLING
WATER FLOW
PARTICLE SIZE
DECOMPOSITION
pH
REDOX
MINOR NUTRIENTS
ORGANIC MATTER
COAGULATION
DEATH
EXCRETION
WATERSHED
PARTICULATE PHOSPHORUS
RESUSPENSION
SETTLING
ATMOSPHERE
BACTERIA
FUNGI
WATER MOVEMENT
OXYGEN
HARDNESS
REDOX
pH
NUTRIENT PUMPING
DEPTH
MIXING
SETTLING
DIFFUSION
DIFFUSION
RESUSPENSION
SEDIMENT PHOSPHORUS

Fig. 10.9. Phosphorus flows and interactions in aquatic systems. Major biotic and nutrient pools are shown in compartments. Lines indicate material flows, with the controls on these flows also indicated. Single headed arrows are used when the opposite directions of flow are labelled.

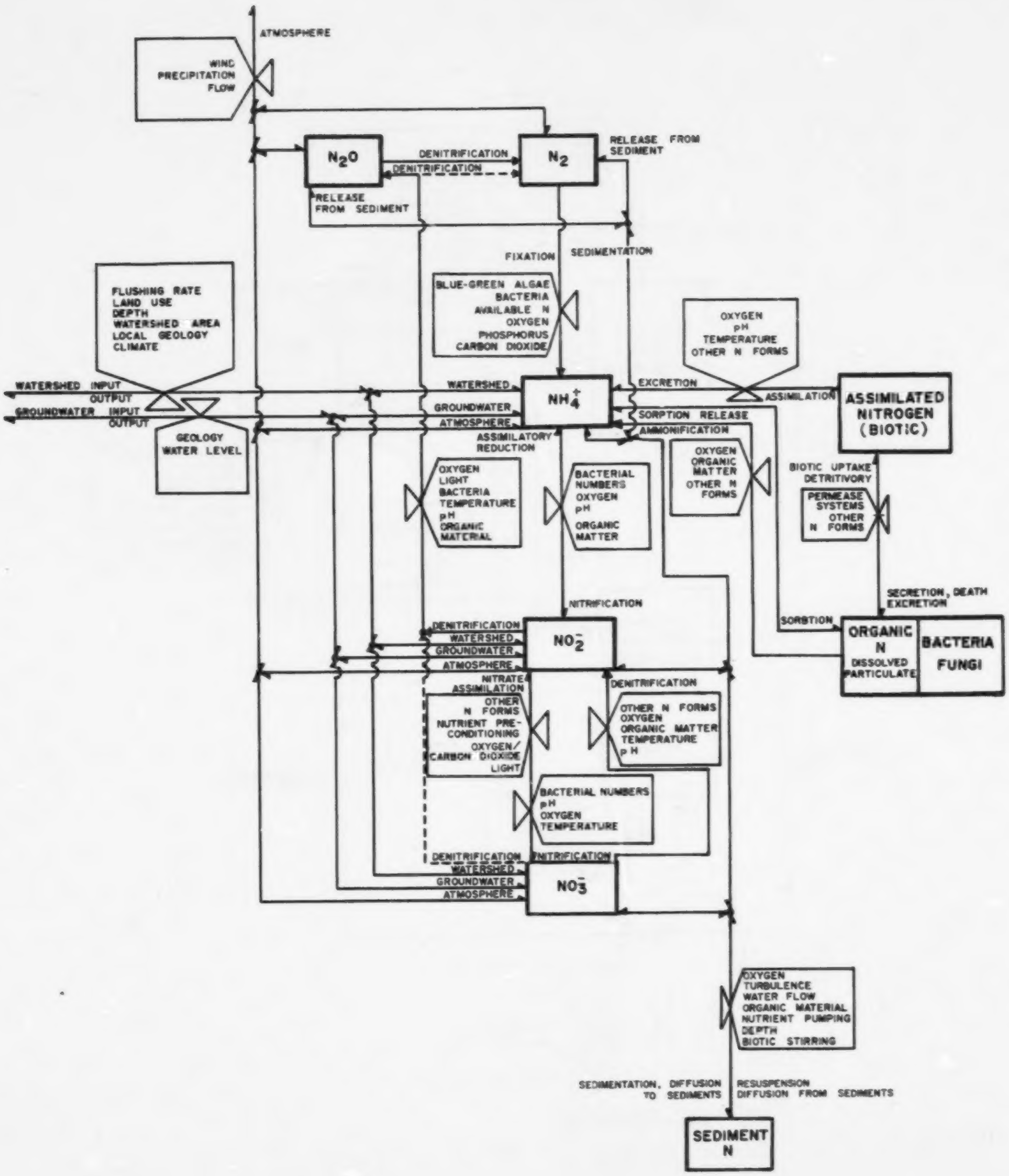
ATMOSPHERE
WIND
PRECIPITATION
FLOW
N_2O
DENITRIFICATION
DENITRIFICATION
N_2
RELEASE FROM SEDIMENT
RELEASE FROM SEDIMENT
FIXATION
SEDIMENTATION
BLUE-GREEN ALGAE
BACTERIA
AVAILABLE N
OXYGEN
PHOSPHORUS
CARBON DIOXIDE
FLUSHING RATE
LAND USE
DEPTH
WATERSHED AREA
LOCAL GEOLOGY
CLIMATE
OXYGEN
pH
TEMPERATURE
OTHER N FORMS
WATERSHED INPUT
OUTPUT
GROUNDWATER INPUT
OUTPUT
GEOLOGY
WATER LEVEL
WATERSHED
GROUNDWATER
ATMOSPHERE
NH_4^+
EXCRETION
ASSIMILATION
SORPTION RELEASE
AMMONIFICATION
ASSIMILATORY REDUCTION
ASSIMILATED NITROGEN (BIOTIC)
OXYGEN
LIGHT
BACTERIA
TEMPERATURE
pH
ORGANIC MATERIAL
BACTERIAL NUMBERS
OXYGEN
pH
ORGANIC MATTER
OXYGEN
ORGANIC MATTER
OTHER N FORMS
BIOTIC UPTAKE
DETRITIVORY
PERMEASE SYSTEMS
OTHER N FORMS
NITRIFICATION
SECRETION, DEATH
EXCRETION
SORBTION
DENITRIFICATION
WATERSHED
GROUNDWATER
ATMOSPHERE
NO_2^-
ORGANIC N
DISSOLVED
PARTICULATE
BACTERIA
FUNGI
NITRATE ASSIMILATION
OTHER N FORMS
NUTRIENT PRE-CONDITIONING
OXYGEN/
CARBON DIOXIDE
LIGHT
DENITRIFICATION
OTHER N FORMS
OXYGEN
ORGANIC MATTER
TEMPERATURE
pH
BACTERIAL NUMBERS
pH
OXYGEN
TEMPERATURE
DENITRIFICATION
NITRIFICATION
WATERSHED
GROUNDWATER
ATMOSPHERE
NO_3^-
OXYGEN
TURBULENCE
WATER FLOW
ORGANIC MATERIAL
NUTRIENT PUMPING
DEPTH
BIOTIC STIRRING
SEDIMENTATION, DIFFUSION TO SEDIMENTS
RESUSPENSION
DIFFUSION FROM SEDIMENTS
SEDIMENT N

Fig. 10.10. Nitrogen flows and interactions in aquatic systems. Major biotic and nutrient pools are shown in compartments. Solid lines indicate material flows, with the controls on these flows also indicated. Dotted lines represent possible directions of flow. Single headed arrows are used when the opposite directions of flow are labelled.

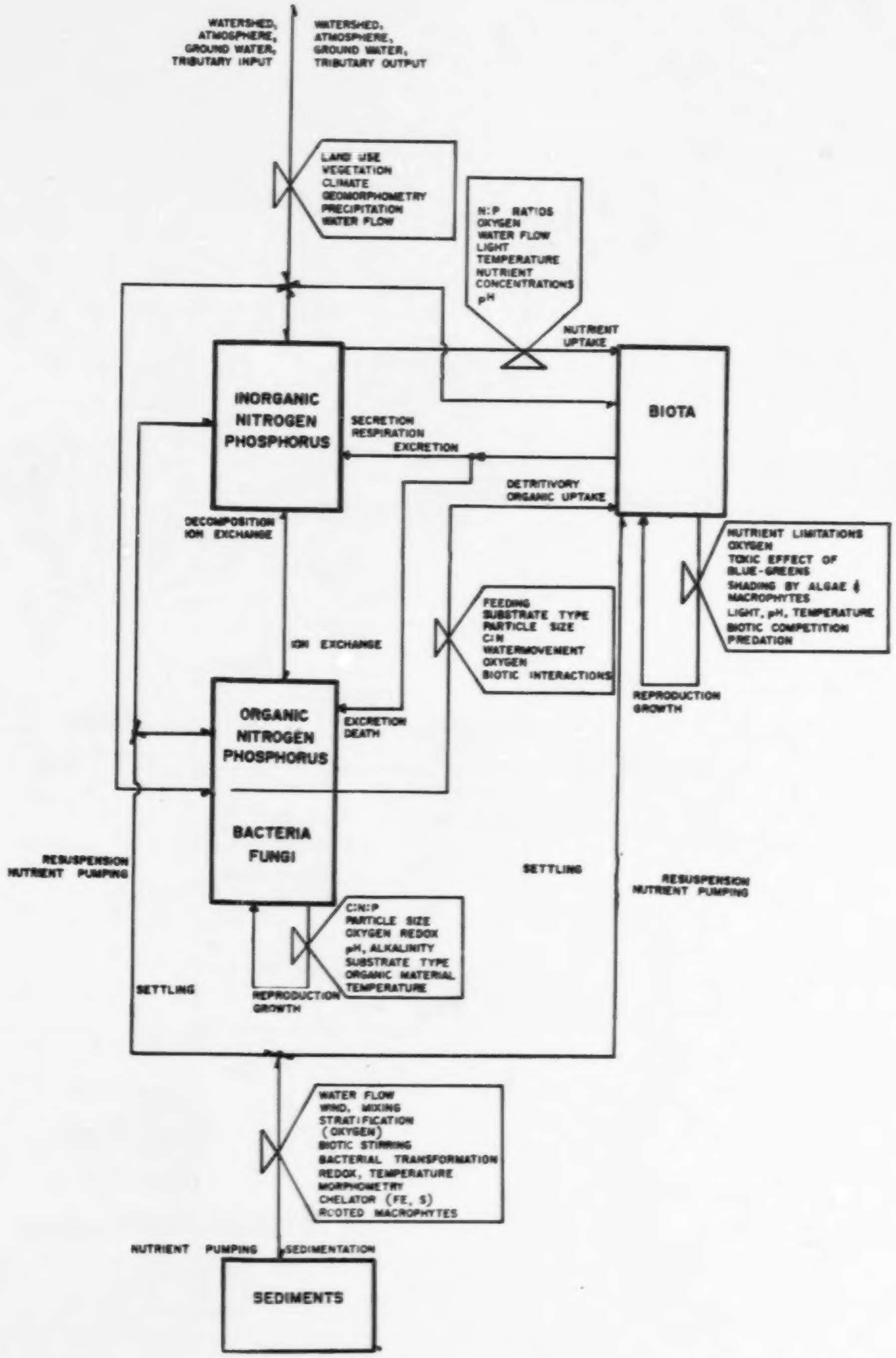
WATERSHED,
ATMOSPHERE,
GROUND WATER,
TRIBUTARY INPUT
WATERSHED,
ATMOSPHERE,
GROUND WATER,
TRIBUTARY OUTPUT
LAND USE
VEGETATION
CLIMATE
GEOMORPHOMETRY
PRECIPITATION
WATER FLOW
N:P RATIOS
OXYGEN
WATER FLOW
LIGHT
TEMPERATURE
NUTRIENT
CONCENTRATIONS
pH
NUTRIENT
UPTAKE
INORGANIC
NITROGEN
PHOSPHORUS
SECRETION
RESPIRATION
EXCRETION
BIOTA
DETRITIVORY
ORGANIC UPTAKE
DECOMPOSITION
ION EXCHANGE
NUTRIENT LIMITATIONS
OXYGEN
TOXIC EFFECT OF
BLUE-GREENS
SHADING BY ALGAE &
MACROPHYTES
LIGHT, pH, TEMPERATURE
BIOTIC COMPETITION
PREDATION
FEEDING
SUBSTRATE TYPE
PARTICLE SIZE
C:N
WATERMOVEMENT
OXYGEN
BIOTIC INTERACTIONS
ION EXCHANGE
REPRODUCTION
GROWTH
ORGANIC
NITROGEN
PHOSPHORUS
EXCRETION
DEATH
BACTERIA
FUNGI
RESUSPENSION
NUTRIENT PUMPING
SETTLING
RESUSPENSION
NUTRIENT PUMPING
C:N:P
PARTICLE SIZE
OXYGEN REDOX
pH, ALKALINITY
SUBSTRATE TYPE
ORGANIC MATERIAL
TEMPERATURE
SETTLING
REPRODUCTION
GROWTH
WATER FLOW
WIND, MIXING
STRATIFICATION
(OXYGEN)
BIOTIC STIRRING
BACTERIAL TRANSFORMATION
REDOX, TEMPERATURE
MORPHOMETRY
CHELATOR (FE, S)
ROOTED MACROPHYTES
NUTRIENT PUMPING
SEDIMENTATION
SEDIMENTS

Fig. 10.11. A conceptual model of combined phosphorus and nitrogen flows and interactions. Major biotic and nutrient pools are shown in compartments. Lines indicate material flows, with the controls on these flows also indicated. Single headed arrows are used when the opposite directions of flow are labelled.

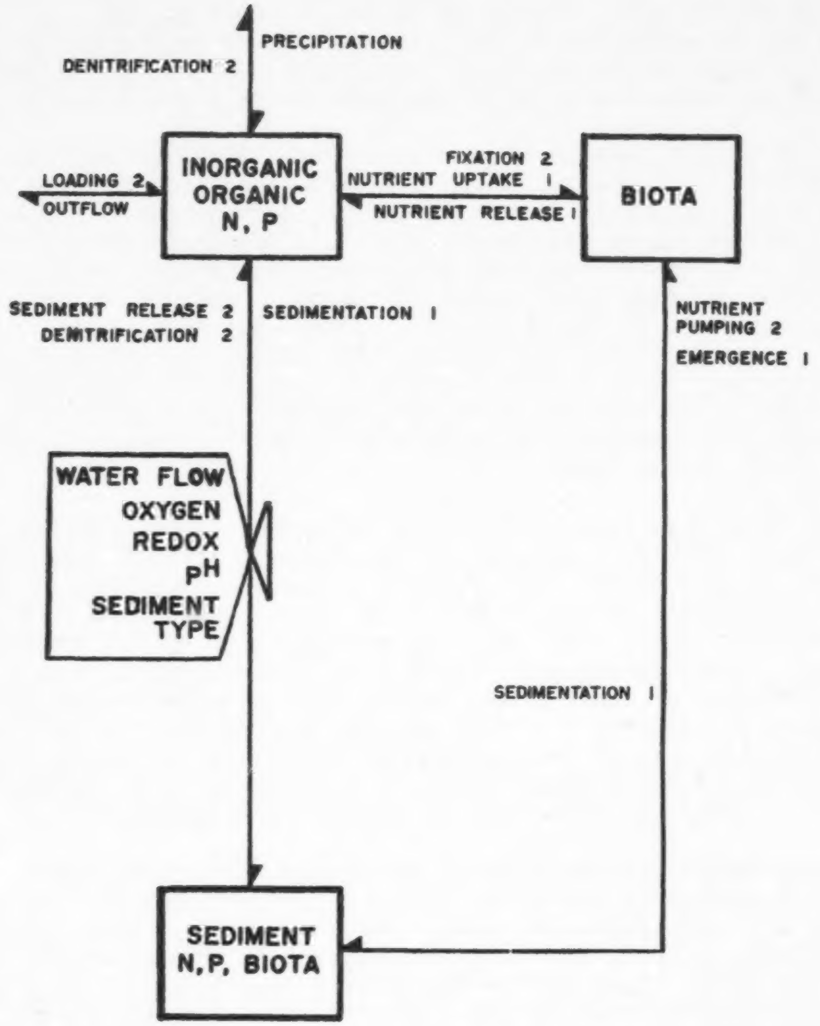
PRECIPITATION
DENITRIFICATION 2
INORGANIC ORGANIC N, P
LOADING 2
OUTFLOW
FIXATION 2
NUTRIENT UPTAKE 1
NUTRIENT RELEASE 1
BIOTA
SEDIMENT RELEASE 2
DENITRIFICATION 2
SEDIMENTATION 1
NUTRIENT PUMPING 2
EMERGENCE 1
WATER FLOW
OXYGEN
REDOX
pH
SEDIMENT TYPE
SEDIMENTATION 1
SEDIMENT N, P, BIOTA

Fig. 10.12. Standard aquatic response to nutrients for various trophic states. Major biotic and nutrient pools are shown in compartments. Solid lines indicate material flows, with the controls on these flows also indicated. Flows followed by a 1 are significant in oligotrophic and eutrophic systems. Flows followed by a 2 are most important in eutrophic systems.

macrophytes, rather than phytoplankton, may be responsible for most of the primary productivity. Increased decomposiiton associated with increased production, as well as increased nitrification, may deplete oxygen levels in the hypolimnion, especially in shallow, stagnant systems. Reduced oxygen concentrations observed in the transition from oligotrophy to eutrophy may eliminate all fish species or result in changes in the dominant species. Fish populations also may be responding to decreased numbers of zooplankton which are unable to graze on blue-green algae. With reduced conditions in the hypolimnion, the sediments may release nutrients to the overlying water.

Nutrient loading over an extensive length of time may build up a vast nutrient reserve in sediments. Under specific conditions sediment nutrients can be the most significant driving force of biotic processes. Diverting sewage in Lake Washington did result in a shift from nutrient rich conditions and high productivity to conditions exhibiting less productivity. However, Lake Washington had only recently become eutrophic and did not have a large build up of nutrients in the sediments. Waters that have exhibited eutrophic conditions for long time periods may be less likely to revert back to more pristine conditions when nutrient loading is reduced. On the other hand, nutrients that have accumulated over long time periods in sediments may be more refractory and permanently unavailable for biotic consumption as was shown in Lake Norrviken (Ahlgren 1977).

Biotic recycling, especially in nutrient rich waters, also may be responsible for maintaining high nutrient levels observed in some lakes (Shapiro et al. 1975; Shapiro 1977). Consideration of mechanisms acting to prevent internal loading might be necessary for successful management. Besides controlling nutrient inputs some ideas for management of aquatic productivity may include: 1) manipulation of higher trophic levels which have a large degree of influence of lower levels (addition of zooplankton, particularly filter-feeders or adjustment of fish species or numbers; 2) control of dominant phytoplankton species (decreasing pH, or addition of CO_2 or nitrogen, thereby selecting against blue-greens); or 3) alteration of the physical environment (increasing circulation or oxygen levels)(Shapiro et al. 1975).

Some management consideration of particular biotic species may be necessary. Systems with equivalent levels of productivity will not necessarily have the same species of biota. Particularly in highly eutrophic lakes this phytoplankton-zooplankton relationship depends on species composition (Vollenweider 1976). Some species may be more desirable than others, and endangered species may need special consideration. Although primary productivity may be predicted by a knowledge of nutrient loading levels, species composition and the impact on a particular species cannot be as easily predicted. Therefore, it is likely that a standard, nationwide management approach to regulate eutrophication of surface waters is not feasible. The problem may be better assessed by a regional and hierarchical organization.

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CHAPTER 11

UTILIZATION OF A HIERARCHICAL SYSTEM TO EVALUATE THE IMPACT OF SEDIMENT AND NUTRIENTS ON FRESHWATER ECOSYSTEMS

The impact of nutrients and sediment on freshwater biota may best be evaluated by the use of a hierarchy of ecological organization. For this report the hierarchical levels of interest are the region, watershed, community, population, and individual. In addition to organizing current information, this scheme may help to identify new directions for research or indicate weaknesses in our knowledge. For example, limnological studies have emphasized individual and population studies; relatively fewer studies of aquatic communities or studies integrating watershed influences on aquatic biota are available. An integrative approach will lead to an understanding of the dynamic behavior of the water body, as well as elucidating the indirect impacts of nutrient and sediment addition on organisms.

The set of characteristics used to describe impact depends upon the level of ecological organization chosen for study. For instance, a comparison of aquatic systems in different regions requires information on climatic, geologic, and vegetational differences which may affect system response. A comparison of aquatic systems within a given region (the watershed level) may require information on primary productivity, sediment and nutrient loading, food chain structure, trophic state, and other system properties. Impact analysis at the community level might use data on species diversity, community respiration or production, and biomass. On the other hand, if biota are defined as populations, then the points of interest might be density, mortality, changes in growth or metabolic patterns, and energetics. Consideration of the individual organism may require, in addition to the population level analysis, information on mortality for different age classes of a species due to some perturbation. However, the set of characteristics needed to be measured are much more easily identified than are the best methods of obtaining the measurements. Presently, information obtained through the use of a variety of methods and indices is compared, reducing the reliability of conclusions.

We also have concluded that all water bodies cannot be managed using one criterion and that different criteria are required for different levels of organization. This is true when the desired state of the community ecosystem and the state of species of interest are different. The principle of community stability contends that the species may shift in presence, abundance, and activity while the community properties stay within set limits. A water body managed so that the impacts of nutrients and sediment do not drive the system out of a set limit of behavior does not necessarily mean that all species will stay within their limits of optimal behavior. On the other hand, the system may be manipulated to maximize production of a particular species. The management of a water body so that a species of interest is undisturbed can result in a change in overall system behavior.

This conflict in the objectives is familiar in resource management. Resolution of the problem requires the following approach: nationwide standards can be used for freshwaters, but these standards may be inexact for certain waters and rather rigid for others. The use of regional standards may ameliorate this problem. It might be possible to set standards for separate, major river basins. At a more detailed level, waters might be set aside for different purposes. For example, some waters may be managed to yield specific system properties which can be defined publicly as clean water. Other waters could be managed for species or characteristics of interest. In some cases both management objectives will coincide and in other cases they will conflict, but by use of a hierarchical system of organization the extent of the conflict can be reduced. Through the implementation of our hierarchical scheme, the important processes at each level can be identified and some management strategies suggested.

11.1 REGIONAL LEVEL

Regionalization provides an organization of patterns in behavioral response of aquatic systems over a wide range of environmental conditions. The biological information obtained to date is weak since various regions have been studied much more than others. For example, in northern regions, especially in the Midwest and Northeast, a good deal of data is available on the ecology of lakes and streams. The southern and western portions of the nation have relatively fewer data. This unevenness in information means that a comparison of response and prediction of impact across the United States is severely limited.

We have made a detailed study of patterns of nutrient, sediment, alkalinity, and land use in the United States using Bailey's ecoregion system. We used the province level in the ecoregion analysis. The province by province analysis shows no clear pattern of differences; however, when provinces are combined, general patterns emerge. Natural differences in nutrient and sediment loading from watersheds may result from different soil types or from the amount and frequency of rainfall. The patterns observed also result from local ecological succession and the climax vegetation. For example, provinces with a high proportion of land in forests show relatively low sediment and phosphorus concentrations, and often lower nitrogen levels in streams than provinces with a high proportion of the land in agriculture. While almost no climax vegetation remains in most provinces, nevertheless, those with a forest climax eventually return to forest when agricultural or other cultural uses of the land are abandoned. Thus, the tendency in these provinces is a return to the climax state typical for them which results in low sediment, low phosphorus, and often low nitrogen in surface waters. For contrast, provinces where the climax is grass and desert vegetation, abandonment of agriculture results in a system which can be used for extensive grazing. Overgrazing is similar to the impact of agriculture, and the high sediment, high phosphorus, and high nitrogen patterns are retained.

Natural differences in alkalinity also will influence the biotic composition and the response of the system to nutrient impact. For example, softwater systems predominating the Southeast and extreme Northwest have low productivity and may have a higher nutrient loading tolerance since bacterial transformations are inhibited. Hardwater systems, prevailing in the Midwest and Southwest generally are low in productivity. Productivity in these areas may be suppressed by high sediment levels or by organic-inorganic interactions that bind phosphorus, making it unavailable for biota. Of course, cultural practices such as the use of fertilizers and urban outputs also can affect these patterns.

Regionalization might provide a means by which management of aquatic resources of the entire United States may be accomplished. Whether or not regional management is useful must await studies of poorly known areas, comparisons between regions and system types, and adoption of the most appropriate regional scheme.

11.2 WATERSHED AND COMMUNITY LEVELS

The behavior of biota in a water body is inseparable from events occurring in the watershed. Disturbances in the watershed increase the amount and influence the type of sediment and nutrient loading to the water. The extent to which biota are impacted by sediment and nutrients depends on the magnitude of inputs and outputs, the trophic state of the system, and the biotic composition of the system.

High levels of sediment can be detrimental to producers as well as consumer species. As sediment becomes suspended, light penetration is reduced and primary production may decline. Nutrients associated with sediment entering the water from runoff may stimulate production. This stimulation may offset the detrimental effect of sediment, as long as high levels of sediment are not suspended. When flow rates are high, biota may be affected by sediment scour, abrasion, or burial. Suspended sediment exerts the greatest impact in slower flowing systems where it impedes primary production by reducing light penetration. Bed load movement is more of a problem in faster flowing systems where it physically damages benthic organisms.

The watershed also provides the major source of nutrients to the water body. An autotrophic system may respond to nitrogen or phosphorus inputs, or both, depending upon the initial nutrient ratios in the system. The direct impact of nutrients is the stimulation of primary productivity. Higher trophic levels may be affected indirectly by nutrient additions through two different mechanisms: the impact may result from changes in the physicochemical environment associated with increased primary production or may be determined by the number of steps away from the primary producers in the feeding web. In heterotrophic systems community productivity may be increased by addition of nitrogen, which stimulates decomposition.

In lakes the dominant primary producers are a major determinant of other biota present in the system. Autochthonous sources of nutrients are most important in slow moving aquatic ecosystems, which are large in volume in comparison to the watershed area. In lakes, both autochthonous and allochthonous nutrient inputs modify the composition of primary producers and thereby the composition of other trophic levels. Depending on the plants which become dominant, an increase in primary production may increase or decrease the productivity of higher trophic levels. In contrast, in many streams, the amount and composition of allochthonous organic material inputs will determine the types and numbers of organisms present in the system. Certain organic inputs may increase the resource base of aquatic animals, whereas an excess of easily decomposable materials may cause oxygen depletion and feeding inhibitions.

A primary physical factor influencing the degree of impact of nutrients on biota is water residence time, which is an indication of the dilution of the incoming nutrients. Thus, the rate of flushing determines the extent to which a system can tolerate nutrient loading. Permissible nutrient loading levels, based on hydraulic residence time, have been proposed for the maintenance of different trophic states (Vollenweider and Dillon 1974; Vollenweider 1976). If a system has a low flushing rate, or if it is highly eutrophic, internal nutrient sources may be significant, and the predictability of the trophic state may decrease.

Indirect effects on biota, although often overlooked, also are of interest; therefore, the degree to which impact is propagated thorough an ecosystem foodweb must be considered. Impact on fish, zooplankton, and aquatic invertebrates is often the result of indirect effects such as oxygen depletion, nutrient enrichment, changes in food resource composition and diversity, habitat modification, and toxic effects of blue-green algae. Impact may be transmitted through several links of a food web before affecting trophic levels removed from the point of direct impact. Because aquatic ecosystems are circularly causal (Hutchinson 1948), the indirect response of higher trophic levels may feed back and affect primary producers. Mathematical models and various systems analysis techniques provide a means by which the indirect influence of nutrients and sediment on biota can be examined.

11.3 POPULATION LEVEL

Prediction of the response of a particular group of organisms (i.e., blue-green algae) to nutrient addition may be possible. However, in most cases prediction of a species' response is more difficult. An aquatic system is a network of interacting organisms and physico-chemical processes; the response of any species is constrained by its position in the system network relative to system components which impinge upon it. Results of laboratory experiments can only be applied loosely to field conditions because of the confounding variables which cannot be controlled in the environment. Even the response of one species in two adjacent water bodies may be different as a result of varying environmental parameters. Detailed mathematical models such as MS. CLEANER (Park et al. 1978) may provide a means of predicting impact on individual groups of organisms, although the detail required to predict a species' response may be too unwieldy.

The response of individual species to nutrients conventionally has been examined under the laws first recognized by Justus Liebig. Liebig's Law of the Minimum (1840) states that the factor in shortest supply will limit the growth of a population if physical conditions are optimal. Liebig's Law recognizes a portion of a response curve which describes the response of output of a system to a change in input of one essential factor. In this positive slope portion of the performance curve, addition of the limiting factor stimulates the response. At very high inputs, even though the factor may no longer be limiting, a negative response may occur as the factor becomes toxic or as a competitor species becomes dominant. The data in the response or performance curve are required in a system model for prediction of impact in order to describe the relationship of one component to another and one component to the environment.

Liebig's Law can and has been applied to the response of an entire aquatic system, but Lane and Levins (1977) have questioned whether this is justified because systems are typically composed of many interacting species with different physiological responses. However, we feel that justification of applying Liebig's Law to the response of an entire system can be made. Even though individual responses are varied, the overall response of the interacting network of an aquatic system is predictable. Addition of nitrogen, phosphorus, or both, may positively influence some species, negatively influence others, or have no effect. Certain species may act to compensate for the negative response of other species such that system productivity increases. Qualitative network analyses (Lane and Levins 1977; Hill 1979) can be used to trace influence through a network to determine the direction of a whole system response. Quantitative prediction can be done using mathematical models. The mechanisms for nutrient limitations on a composite phytoplankton community have been dealt with in recent aquatic system models (Chen and Orlob 1975; DiToro et al. 1975; Park et al. 1975; Patten et al. 1975).

11.4 INDIVIDUAL LEVEL

From physiological studies on individual organisms, tolerance limits have been established for many aquatic species. Species which have narrow tolerance ranges can be used as indicators of water quality and water quality change. Although the presence of an individual species may not be predictable, its absence may be. The use of indices based on species diversity where taxonomy is known or based on diversity of broad functional groups may provide a great deal of information concerning the condition of the aquatic system.

11.5 USE OF MODELS

Understanding the impact of nutrients and sediment in aquatic ecosystems can be facilitated by conceptual and mathematical models. Models are used to organize information about complex systems and to predict the direction and degree of change in selected variables. Coarse resolution characteristics of an ecosystem such as trophic state and primary production rates often can be predicted with a few easily measured variables. Among the most important of these are flushing rate, nutrient and sediment loadings, initial trophic state, and movement to and from sediments. These parameters determine a response surface which describes the variation of predicted variables. Coarse resolution models have been used to predict the response of a number of lakes (Vollenweider 1972, 1976) and rivers (Streeter and Phelps 1925; O'Connor 1961).

More detailed questions about the chemical and biotic dynamics of aquatic ecosystems can be addressed with finer resolution models. Fine resolution mathematical models incorporate the dependency network which links biotic and chemical components of an ecosystem; both direct and indirect effects of impact can be evaluated. The impact of nutrients and sediment on ecosystem components and processes have been quantitatively predicted for lakes and reservoirs (Chen and Orlob 1975; DiToro et al. 1975; Patten et al. 1975; Park et al. 1978), swamps (Kadlec 1978; Odum 1978), and rivers (Boling et al. 1975; McIntire and Colby 1978).

A premise of this report is that the response of aquatic ecosystems is largely defined by the nature and magnitude of inputs and outputs as well as the internal cycling. Although the importance of inputs from the surrounding watershed in determining aquatic ecosystem behavior has been recognized, watershed behavior is rarely reflected in mathematical models. Outputs also are important in defining ecosystem behavior in impact analysis. Internal mechanisms such as sedimentation and resuspension rates have been shown to be important in determining availability of nutrients to biota. Both outputs and internal cycling must be considered in any predictive model.

By examining aquatic ecosystem models, we have identified components and processes which have been used to predict and describe the response of aquatic ecosystems to nutrient and sediment inputs. The categories of components and processes include biotic and chemical compartments, inputs and outputs, physical and chemical controlling variables, spatial structure and terrestrial-aquatic interactions. Using these components and processes, we have constructed several conceptual models; these models have been used to organize information in the literature and to establish ecosystem networks necessary for qualitative prediction of impact of phosphorus, nitrogen, and sediment inputs. Quantitative prediction of impact on biota can be done using the mathematical models discussed in Chapter 7.

We have constructed the models at two levels of resolution. At the coarser level, macroscopic properties of ecosystems have been used to organize information about impact analyses (see Fig. 10.6). Sediment, nutrients, and biota are the ecosystem components identified at this level of resolution. At the finer level of resolution, sediment, inorganic nutrients, particulate organic materials, macrophytes, bacteria and fungi, vertebrates, invertebrates, and algae have been identified (Fig. 11.1). Information and variables required for impact analyses depend on the questions asked of the system and the objective which the impact analysis is designed to meet.

11.6 LITERATURE CITED

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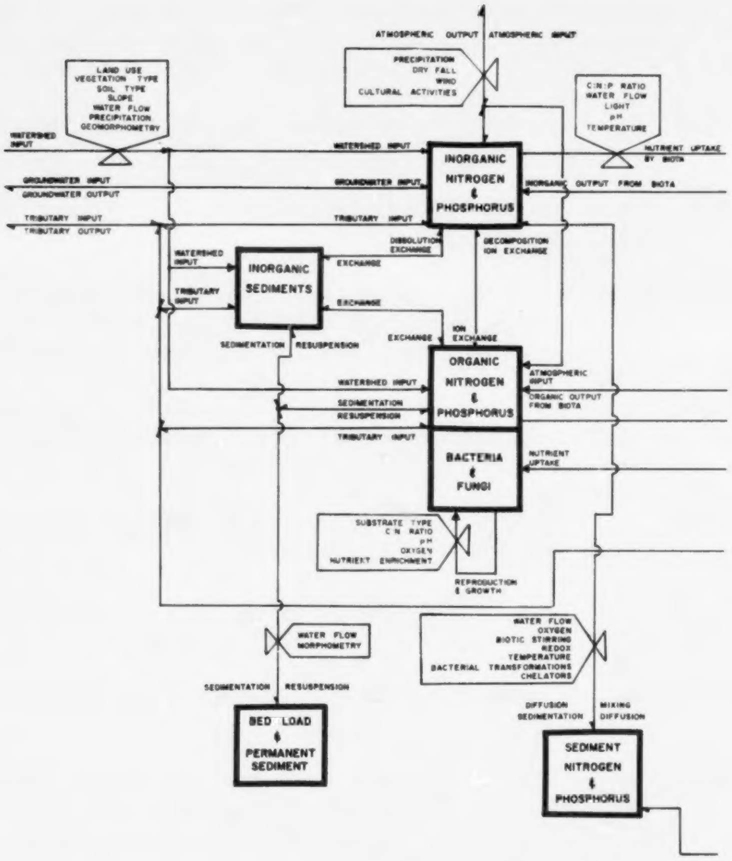
ATMOSPHERIC OUTPUT
ATMOSPHERIC INPUT
PRECIPITATION
DRY FALL
WIND
CULTURAL ACTIVITIES
LAND USE
VEGETATION TYPE
SOIL TYPE
SLOPE
WATER FLOW
PRECIPITATION
GEOMORPHOMETRY
C:N:P RATIO
WATER FLOW
LIGHT
pH
TEMPERATURE
WATERSHED INPUT
WATERSHED INPUT
INORGANIC NITROGEN & PHOSPHORUS
NUTRIENT UPTAKE BY BIOTA
GROUNDWATER INPUT
GROUNDWATER OUTPUT
GROUNDWATER INPUT
INORGANIC OUTPUT FROM BIOTA
TRIBUTARY INPUT
TRIBUTARY OUTPUT
TRIBUTARY INPUT
DISSOLUTION EXCHANGE
DECOMPOSITION ION EXCHANGE
WATERSHED INPUT
INORGANIC SEDIMENTS
EXCHANGE
TRIBUTARY INPUT
EXCHANGE
EXCHANGE
ION EXCHANGE
SEDIMENTATION
RESUSPENSION
ORGANIC NITROGEN & PHOSPHORUS
ATMOSPHERIC INPUT
WATERSHED INPUT
ORGANIC OUTPUT FROM BIOTA
SEDIMENTATION
RESUSPENSION
TRIBUTARY INPUT
BACTERIA & FUNGI
NUTRIENT UPTAKE
SUBSTRATE TYPE
C:N RATIO
pH
OXYGEN
NUTRIENT ENRICHMENT
REPRODUCTION & GROWTH
WATER FLOW
MORPHOMETRY
WATER FLOW
OXYGEN
BIOTIC STIRRING
REDOX
TEMPERATURE
BACTERIAL TRANSFORMATIONS
CHELATORS
SEDIMENTATION
RESUSPENSION
DIFFUSION
SEDIMENTATION
MIXING
DIFFUSION
BED LOAD & PERMANENT SEDIMENT
SEDIMENT NITROGEN & PHOSPHORUS

Fig. 11.1. A conceptual model of biotic, sediment, and nutrient interactions at a fine level of resolution. Major biotic, sediment, and nutrient pools are shown in compartments. Solid lines indicate material flows, with the controls on these flows also indicated. Single-headed arrows are used when the opposite directions of flow are labelled.

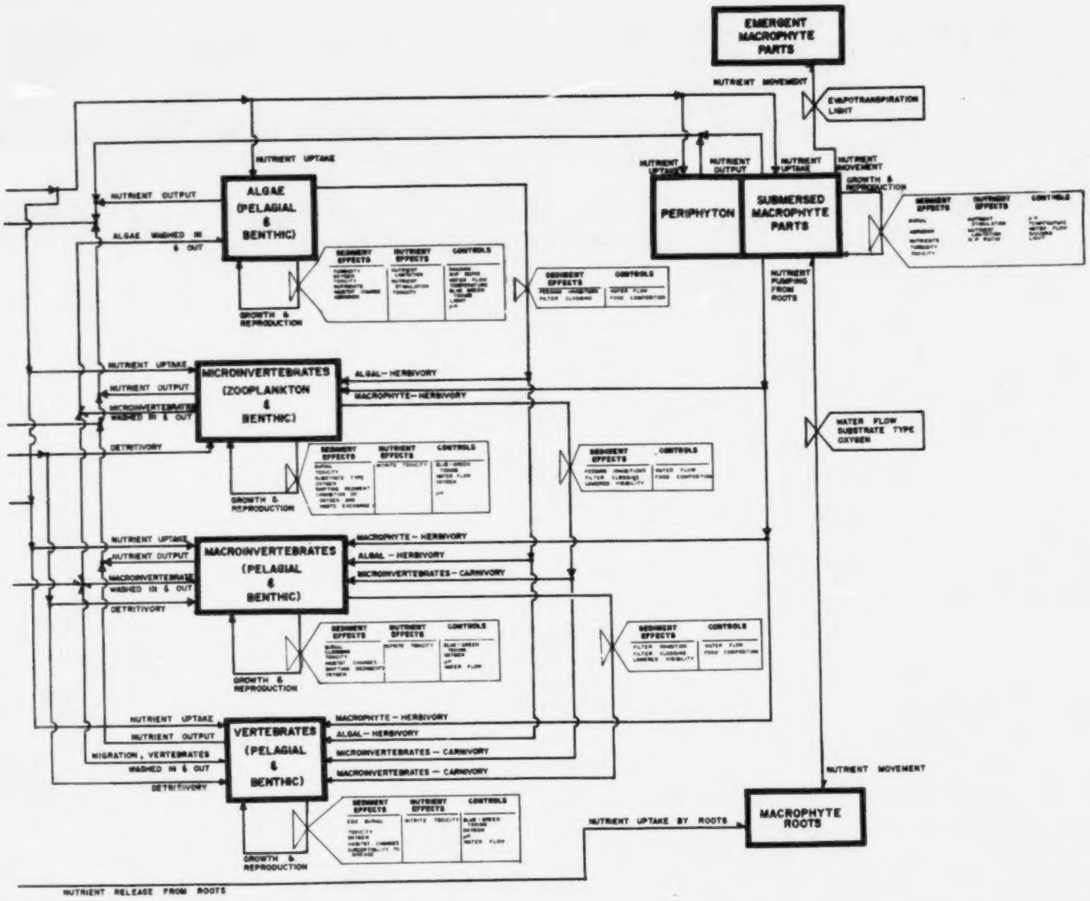
EMERGENT MACROPHYTE PARTS
NUTRIENT MOVEMENT
EVAPOTRANSPIRATION
LIGHT
NUTRIENT UPTAKE
NUTRIENT OUTPUT
NUTRIENT UPTAKE
NUTRIENT MOVEMENT
GROWTH & REPRODUCTION
PERIPHYTON
SUBMERSED MACROPHYTE PARTS
SEDIMENT EFFECTS
NUTRIENT EFFECTS
CONTROLS
BURIAL
ABRASION
NUTRIENTS
TURBIDITY
TOXICITY
NUTRIENT STIMULATION
NUTRIENT LIMITATION
N:P RATIO
pH
TEMPERATURE
WATER FLOW
SHADING
LIGHT
NUTRIENT PUMPING FROM ROOTS
NUTRIENT UPTAKE
NUTRIENT OUTPUT
ALGAE WASHED IN & OUT
ALGAE (PELAGIAL & BENTHIC)
SEDIMENT EFFECTS
NUTRIENT EFFECTS
CONTROLS
TURBIDITY
OXYGEN
TOXICITY
NUTRIENTS
HABITAT CHANGE
ABRASION
NUTRIENT LIMITATION
NUTRIENT STIMULATION
TOXICITY
SHADING
N:P RATIO
WATER FLOW
TEMPERATURE
BLUE GREEN TOXINS
LIGHT
pH
GROWTH & REPRODUCTION
SEDIMENT EFFECTS
CONTROLS
FEEDING INHIBITION
FILTER CLOGGING
WATER FLOW
FOOD COMPOSITION
NUTRIENT UPTAKE
NUTRIENT OUTPUT
MICROINVERTEBRATES WASHED IN & OUT
DETRITIVORY
MICROINVERTEBRATES (ZOOPLANKTON & BENTHIC)
ALGAL – HERBIVORY
MACROPHYTE – HERBIVORY
SEDIMENT EFFECTS
NUTRIENT EFFECTS
CONTROLS
BURIAL
TOXICITY
SUBSTRATE TYPE
OXYGEN
SHIFTING SEDIMENT
CONDITION OF OXYGEN AND WASTE EXCHANGE
NITRATE TOXICITY
BLUE-GREEN TOXINS
WATER FLOW
OXYGEN
pH
GROWTH & REPRODUCTION
SEDIMENT EFFECTS
CONTROLS
FEEDING INHIBITIONS
FILTER CLOGGING
LOWERED VISIBILITY
WATER FLOW
FOOD COMPOSITION
WATER FLOW
SUBSTRATE TYPE
OXYGEN
NUTRIENT UPTAKE
NUTRIENT OUTPUT
MACROINVERTEBRATES WASHED IN & OUT
DETRITIVORY
MACROINVERTEBRATES (PELAGIAL & BENTHIC)
MACROPHYTE – HERBIVORY
ALGAL – HERBIVORY
MICROINVERTEBRATES – CARNIVORY
SEDIMENT EFFECTS
NUTRIENT EFFECTS
CONTROLS
BURIAL
CLOGGING
TOXICITY
HABITAT CHANGES
SHIFTING SEDIMENTS
OXYGEN
NITRITE TOXICITY
BLUE-GREEN TOXINS
OXYGEN
pH
WATER FLOW
GROWTH & REPRODUCTION
SEDIMENT EFFECTS
CONTROLS
FILTER INHIBITION
FILTER CLOGGING
LOWERED VISIBILITY
WATER FLOW
FOOD COMPOSITION
NUTRIENT UPTAKE
NUTRIENT OUTPUT
MIGRATION, VERTEBRATES
WASHED IN & OUT
DETRITIVORY
VERTEBRATES (PELAGIAL & BENTHIC)
MACROPHYTE – HERBIVORY
ALGAL – HERBIVORY
MICROINVERTEBRATES – CARNIVORY
MACROINVERTEBRATES – CARNIVORY
SEDIMENT EFFECTS
NUTRIENT EFFECTS
CONTROLS
EGG BURIAL
TOXICITY
OXYGEN
HABITAT CHANGES
SUSCEPTIBILITY TO DISEASE
NITRITE TOXICITY
BLUE-GREEN TOXINS
OXYGEN
pH
WATER FLOW
GROWTH & REPRODUCTION
NUTRIENT MOVEMENT
NUTRIENT UPTAKE BY ROOTS
MACROPHYTE ROOTS
NUTRIENT RELEASE FROM ROOTS

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Fig. 11.1. Continued.

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